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Localities of Fossil Vertebrates Obtained from the Niobrara Formation (Cretaceous) of Kansas

BY

DAVID BARDACK

University of Kansas
Lawrence
1965

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Localities of Fossil Vertebrates Obtained from the Niobrara Formation (Cretaceous) of Kansas

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BY

DAVID BARDACK

Fossil vertebrates have been obtained over the years from the Niobrara Formation in western Kansas since 1870. Most of the specimens were obtained between 1875 and 1910. A list of the collectors includes such well-known persons as Barnum Brown, E. C. Case, E. D. Cope, O. C. Marsh, Handel T. Martin, Benjamin F. Mudge, Elmer S. Riggs, Charles H. Sternberg, George F. Sternberg, and Samuel W. Williston. Vetebrates from the Cretaceous of Kansas are in museums throughout Europe and North America. Even the smaller museums display some specimens of Kansas fishes and reptiles. Extensive collections are to be found in the American Museum of Natural History, the Peabody Museum of Natural History at Yale University, the Museum of Natural History at the University of Kansas, the United States National Museum, the Museum of Comparative Zoology at Harvard University, and the Fort Hays Kansas State College Museum.

Abbreviations used in the text beyond for these museums are, respectively, as follows: AMNH, YPM, KU, USNM, MCZ, and FH.

The Niobrara Formation is exposed in a band from west-central to north-central Kansas. The more extensive and paleontologically richer deposits are exposed in Logan, Gove and Trego counties. Graham and Rooks counties to the north and northeast, respectively, of Trego County also have produced fossil vertebrates. Few have been obtained from the scattered, smaller exposures of the Niobrara Formation in the north-central counties (Phillips, Smith and Jewell).

The Niobrara Formation includes two members, the lower Fort Hays limestone and the upper Smoky Hill Chalk. The term Kansas chalk is sometimes applied to the Niobrara Formation and sometimes is limited to the Smoky Hill Chalk member. Most vetebrate fossils are known from the Smoky Hill Chalk.

Catalogue records for the majority of Kansas Cretaceous vertebrates, including nearly all of the type specimens, yield little or no data as to locality other than "western Kansas," "Kansas chalk," "Niobrara Formation," or a particular county. Nevertheless, cata-

logue records for many specimens, especially those in the collections of the University of Kansas Museum of Natural History, indicate by the name of a ranch or creek or number of miles from a town, the site at which a particular fossil was found. More precise locality information would provide valuable data for studies of a stratigraphic or ecological nature. Differences in fossil assemblages from eastern and western exposures might be discovered. Evolutionary changes in certain groups during Niobrara time might be traced.

In the course of studying anatomy and systematics of fossil fishes from the Niobrara Formation I have several times sought the location of such places as "Martin's Canyon," "Robber's Roost" or a site "3 miles North of Monument Rocks." In an effort to provide more adequate locality information I have consulted residents and county engineers of those counties in which chalk beds are exposed, talked with persons who have collected fossils from the chalk, examined U. S. Dept. of Agriculture aerial photographs and geologic maps of pertinent counties, studied old maps and correspondence of collectors and personally examined numerous chalk exposures. I have been able to determine range, township and in many cases section of the poorly defined localities in which early collections were made. It has been my primary interest to ascertain localities that have yielded specimens of fish. Because fossil reptiles and birds in the Niobrara Formation have generally come from the same sites as the fishes, localities of many reptilian and avian specimens may be determined from the information given below.

Locality records of fossils derived from publications or museum catalogues are listed under the name of the museum in which the fossil material is housed. Each locality is numbered for reference purposes within this paper. The numerical listing by county for material at the University of Kansas corresponds to the numerical listing in the locality catalogue of the Division of Vertebrate Paleontology. The original description of a locality is cited first in boldface type followed by a statement of section(s), township, and range as determined in this study. Where exposures from which the fossils were obtained extend across more than one section, two or more sections are cited. Comments on the geologic horizon and geographic position of a locality as originally cited are given if necessary. Estimates of mileage by the older collectors were in many, but not all, instances less than the true mileage.

For assistance in determination of localities I am indebted to George F. Sternberg of Hays, Kansas, Albert O'Toole of Ransom,

Kansas, Myrl V. Walker of Fort Hays Kansas State College Museum, and Marion Bonner of Leoti. Examination of collections was made possible by National Science Foundation Grant No. GB 582.

UNIVERSITY OF KANSAS MUSEUM OF NATURAL HISTORY

Most of the Kansas Cretaceous vertebrates now in the Museum of Natural History were obtained between the years 1895 and 1910 through the efforts of S. W. Williston, H. T. Martin, C. E. McClung and several students including Barnum Brown, E. C. Case, Alban Stewart, Wyman Green, Roy Moodie and E. H. Taylor. The specimens at this museum represent results of the last large-scale effort at collecting Niobrara material for one museum. Locality records for Niobrara specimens at the University of Kansas are more nearly complete than such records are for specimens at the American Museum of Natural History or the Peabody Museum of Natural History. Numbers assigned to localities under each county name correspond to numbers in the locality catalogue of the Division of Vertebrate Paleontology at the University of Kansas.

A. *Gove County*

1. **Near Banner (Bana).** See Trego Co., Locality No. 2.
2. **6 mi. SE Gove City.** Sections 23, 24, T. 13 S, R. 28 W.
3. **Sec. 5, T. 13 S, R. 35 W.** Locality uncertain. R. 35 W would be in Logan County but chalk beds are not exposed in the section cited. R. 25 W in Trego County also would be outside of the chalk beds.
4. **Plum Creek.** This stream runs SE into the Smoky Hill River. Exposures near the junction of Plum Creek and the Smoky Hill River in T. 15 S, R. 28 W have been worked by several collectors according to Myrl V. Walker.
5. **Martin's Canyon.** Sections 14, 15, 22, 23, 26, 27, 35, T. 14 S, R. 26 W. According to Albert O'Toole and George Sternberg this canyon (or pair of north-south canyons) carries the first tributary of the Smoky Hill River lying entirely within Gove County. The fossils probably came from the eastern ravine; it crosses sections 14, 23 and 26.
6. **Spencer's Canyon.** Sections 17, 20, 29, T. 14 S, R. 25 W. This canyon is in Trego County according to Albert O'Toole. A broad, apparently unnamed canyon (eastern vertical tier of sections in T. 14 S, R. 26 W) is crossed by the Gove-Trego county line. This canyon might have been confused with Martin's Canyon or Spencer's Canyon by some collectors.
7. **4 mi. SE Elkader.** Sec. 13 and/or 24, T. 15 S, R. 32 W, in Logan County.
8. **4 mi. SE Gove City.** Sections 16, 17, T. 13 S, R. 28 W.
9. **6 mi. SW Gove City.** Sections 28, 29, T. 13 S, R. 29 W.
10. **6 mi. W Castle Rock.** Sec. 35, T. 13 S, R. 27 W.
11. **Spicer's Ranch, SW Castle Rock.** Spicer's Ranch was in sec. 10, T. 13 S, R. 26 W. This is NW of Castle Rock. Several fossil vertebrates have been obtained from sec. 16, T. 13 S, R. 26 W on the Andrew Bird ranch.
12. **S side Smoky Hill River.** Locality cannot be determined.
13. **E Spencer's Canyon.** This canyon is in Trego Co. See Gove Co., Locality No. 6.

14. **S side Smoky Hill River and Martin's Canyon.** Numerous exposures in northeastern sections of T. 15 S, R. 26 W.
15. **1½ mi. W Castle Rock.** Sec. 3, T. 14 S, R. 26 W.
16. **4 mi. N and E of Castle Rock, Perrington Ranch.** Sec. 8 or 9, T. 14 S, R. 25 W. This locality is in Trego Co. on the Purinton Ranch.
17. **Monument Rocks.** Sec. 34, T. 14 S, R. 31 W.
18. **2 mi. E Monument Rocks.** Sections 25, 26 or 34, 35, T. 14 S, R. 31 W.
19. **6 mi. E Gove City on Hackberry Creek.** See Gove Co., Locality No. 2. Hackberry Creek flows SE from Gove City.
20. **N of Monument Rocks.** Locality cannot be determined.
21. **Hell Creek.** Southeastern sections of T. 15 S, R. 31 W. Hell Creek is a tributary of the Smoky Hill River. Another tributary with broad chalk exposures lies just east of Hell Creek. These paleontologically rich exposures (sections 18, 19, 30, 31, T. 15 S, R. 30 W) are called Hell's Bar by George Sternberg. Specimens labelled Hell Creek may have come from Hell's Bar.
22. **2 mi. SW Castle Rock.** W½ sec. 13 and E½ sec. 14, T. 14 S, R. 26 W.
23. **3½ mi. SW Castle Rock.** Sections 22, 23, T. 14 S, R. 26 W.
24. **4 mi. W Castle Rock.** Sec. 5, T. 14 S, R. 26 W and sec. 32, T. 13 S, R. 26 W.
25. **3 mi. N Monument Rocks.** Sections 15, 22, T. 14 S, R. 31 W.

B. *Graham County*

1. **½ mi. NW Hill City.** Sec. 10, T. 8 S, R. 23 W.
2. **1 mi. W Hill City.** See Graham Co., Locality No. 1.
3. **1½ mi. NW Hill City.** NW¼ sec. 10, T. 8 S, R. 23 W.
4. **NW Hill City.** Locality cannot be determined.
5. **6 mi. S Hill City.** Sec. 14, T. 9 S, R. 23 W. Small exposure on bank of stream.
6. **3 mi. NW Hill City, near Solomon River.** ?sec. 17, T. 8 S, R. 23 W. This exposure is within a half mile of the river but W rather than NW of Hill City.
7. **Hill City.** Locality cannot be determined.
8. (Pleistocene locality.)
9. **½ mi E Penokee.** W½ sec. 13 and E½ sec. 14, T. 8 S, R. 24 W. This locality is about 1 mi. E of Penokee.

C. *Logan County* (formerly St. John County)

1. **Butte Creek.** Locality of specimens cannot be determined.
2. **Near Twin Buttes.** Twin Buttes is in NE¼ sec. 1, T. 15 S, R. 37 W.
3. **Lisbon.** Sec. 8, T. 12 S, R. 36 W. This town existed in the early days of the Kansas Pacific (now Union Pacific) Railroad. Sheridan, Kansas, was at approximately the same place. Rocks exposed in the vicinity of Lisbon are lower members of the Pierre Shale.
4. **NE Russell Springs.** T. 13 S, R. 35 W. Small areas of chalk are exposed less than two miles northeast of the town.
5. **Near Russell Springs.** T. 13 S, R. 35 W. Several exposures on the S side of the Smoky Hill River including one ¼ to ½ mile in linear extent known locally as Hell's Half Acre (N½ sec. 27, T. 13 S, R. 35 W) occur near the town.
6. **4½ mi. NW Elkader, Logan Co. line.** Elkader has moved several times, but the town has been at its present location (sec. 34, T. 14 S, R. 32 W) or within a mile of this site during the period in which most of the specimens at the University of Kansas were collected. The Gove-Logan

county line lies NE of Elkader. The position of Locality No. 6 is therefore uncertain.

7. **7 mi. NW Elkader.** Numerous small chalk exposures lie NW of Elkader.
8. **S of Elkader.** Locality cannot be determined.
9. **SE of Elkader.** Locality cannot be determined.
10. **W of Russell Springs.** Numerous exposures in T. 13 S, R. 35 W in sections lying W and SW of the town. See Logan Co., Locality No. 5.
11. **1 mi. N Elkader.** ?sec. 22 or 27, T. 14 S, R. 32 W.
12. **½ mi. E Beaver Creek, Elkader.** T. 15 S, R. 32 W. Beaver Creek (now generally known as Ladder Creek) enters the Smoky Hill River in sec. 34, T. 14 S, R. 35 W. Several extensive exposures of Smoky Hill Chalk are in sec. 12, T. 15 S, R. 32 W. These are 1 to 2 mi. S of Elkader and ½ mi E of Beaver Creek.
13. **2½ mi. NE Elkader.** Sec. 25, T. 14 S, R. 32 W.
14. **Elkader.** Locality of fossils cannot be determined.
15. **5 mi. SW Elkader, Beaver Creek.** Sections 8, 17, T. 15 S, R. 32 W.
16. (Pliocene locality.)
17. (Pleistocene locality.)
18. **12 mi. W Russell Springs.** Sec. 24, T. 13 S, R. 37 W.
19. **Near Elkader.** Locality cannot be determined.
20. **10 mi. SW Russell Springs, Willow Canyon.** Sections 11, 12, 13, T. 15 S, R. 35 W. This locality is S rather than SW of Russell Springs and appears to be identical with the locality termed Cedar Canyon by several present-day collectors according to Marion Bonner.
21. **Beaver Creek.** Locality of fossils cannot be determined.
22. **2 mi. NW Russell Springs.** Sec. 14, T. 13 S, R. 35 W. Small exposures of chalk are along a stream flowing through Russell Springs and into the Smoky Hill River.
23. **Hell Creek.** This stream is in Gove Co. See Gove Co., Locality No. 21.
24. **2½ mi. N Elkader.** ?sec. 15, T. 14 S, R. 32 W.
25. **2½ mi. SE Elkader.** ?sec. 11, T. 15 S, R. 32 W.
26. **Russell Springs.** Locality of fossils cannot be determined.
27. **2 mi. W Russell Springs.** Sec. 27, T. 13 S, R. 35 W. See Logan Co., Locality No. 5.
28. **Smoky Hill River.** Locality of fossils cannot be determined.
29. **NW¼ sec. 20, T. 11 S, R. 14 W, Benton Cretaceous.** R. 14 W would be in Russell County.
30. **McAllister.** Sec. 24, T. 12 S, R. 37 W. Exposures in the vicinity of McAllister are in Pierre Shale.
31. **N point of bluff, E side of Beaver Creek.** T. 15 S, R. 32 W. See Logan Co., Locality No. 12.
32. **Near Lisbon.** See Logan Co., Locality No. 3.

D. *Trego County*

1. **SE Castle Rock.** ?Near Wildcat Canyon. See Trego Co., Locality No. 7.
2. **Banner.** Sec. 29, T. 13 S, R. 25 W. Banner was a Trego Co. Post Office. The Banner Post Office at one time was in sec. 26 and at another time in sec. 32. Section 29 was the more likely reference point for other localities in Trego Co. during the period of field work by the University of Kansas.
3. **2 mi. SE Banner.** W½ sec. 3 and E½ sec. 4, T. 14 S, R. 25 W.
4. **½ mi. SE Banner.** Chalk exposures are more than ½ mi. from Banner. A small exposure (sec. 32, T. 13 S, R. 25 W and sec. 5, T. 14 S, R. 25 W) lies SW of Banner.

5. **SW Gove City.** Gove City is in Gove Co. See Gove Co., Locality No. 9.
6. **Hackberry Creek.** Locality of fossils cannot be determined. Several major exposures of chalk lie close to this creek.
7. **Cat Hills.** S½ sec. 9 and W½ sec. 15 and sec. 16, T. 14 S, R. 25 W. This locality is better known as Wildcat Canyon.
8. **Martin's Canyon.** See Gove Co., Locality No. 5.
9. **1½ mi. S Banner, Cat Hills.** See Trego Co., Locality No. 7.
10. **Bluffs W side Sec. 3.** Sec. 3, T. 14 S, R. 25 W. See Trego Co., Locality No. 3.
11. **E of O'Toole School.** Sections 3 and 10 (along Gibson Creek), T. 15 S, R. 25 W. This school was in sec. 5, T. 15 S, R. 25 W.
12. **½ mi. S O'Toole's.** Sec. 3, T. 15 S, R. 25 W. The O'Toole Ranch is in sec. 34, T. 14 S, R. 25 W.
13. **¼ mi. N Neuenschwander's Ranch, Banner.** SW¼ sec. 10, T. 14 S, R. 25 W. The Neuenschwander Ranch is in sec. 15, T. 14 S, R 25 W.
14. **Near Banner, S of Neuenschwander's.** W½ sec. 15, T. 14 S, R. 25 W.
15. **Near Banner, ½ mi. SW Neuenschwander's.** Sec. 16, T. 14 S, R. 25 W.
16. **1½ mi. SE Neuenschwander's, Banner.** NW¼ sec. 23, NE¼ sec. 22, SE¼ sec. 15, SW¼ sec. 14, T. 14 S, R. 25 W.
17. **¼ mi. S Neuenschwander's.** W½ sec. 15, T. 14 S, R. 25 W.
18. **2½ mi. E Banner.** No chalk is exposed E of Banner. Locality is probably SE of Banner. See Trego Co., Locality No. 19.
19. **2½ mi. SE Banner.** E½ sec. 4, W½ sec. 3, T. 14 S, R. 25 W. *Cf.* Trego Co., Locality No. 3.
20. **¾ mi. N Neuenschwander's near Banner.** E½ sec. 10, T. 14 S, R. 25 W.
21. **4 mi. S Banner, Wildcat Hills.** Sec. 16, T. 14 S, R. 25 W. See Trego Co., Locality No. 7.
22. **2 mi. NW Wakeeney on Saline River.** Chalk exposures are at least 4 mi. NW of Wakeeney. The Saline River is more than 5 mi. from Wakeeney. The locality cannot be determined.
23. **6 mi. NW Wakeeney.** Sections 16, 21, T. 11 S, R. 24 W. Other exposures are developed in sections 10, 15 and 22. This land is part of the E. J. Garrett Ranch.
24. **3 mi. E Banner at Neuenschwander's.** Neuenschwander's is not directly E of Banner. See Trego Co., Locality No. 13. The locality cannot be determined.
25. **1 mi. N Smoky Hill River.** The locality is probably in Spencer's Canyon. See Gove Co., Locality No. 6.
26. **15¾ mi. SW Banner.** This site must be in Gove County. The locality cannot be determined.

E. *Wallace County*

1. **Beaver Creek.** See Logan Co., Locality No. 12.
2. **McAllister.** See Logan Co., Locality No. 30.
3. **Eagle Tail Creek near Sharon Springs.** T. 13 S, R. 40 W. Exposures of Pierre Shale.
4. **Near McAllister.** See Logan Co., Locality No. 30.

FORT HAYS KANSAS STATE COLLEGE MUSEUM

Locality records of fishes and reptiles (listed separately) in the State College Museum are cited. Most of these specimens were collected by George F. Sternberg, Myrl V. Walker and Marion Bonner. Locality numbers do not refer to the State College Mu-

seum catalogue and such numbers are assigned here arbitrarily. Localities that are the same as those in the University of Kansas catalogue are so designated.

Fishes

1. **Bluffs S of Castle Rock.** Sec. 1, T. 14 S, R. 26 W, Gove Co. FH No. 25, type of *Kansius sternbergi* Hussakof.
2. **11 mi. S Quinter.** ?sec. 16, T. 13 S, R. 26 W, Gove Co. FH No. 1649, *Cimolichthys* sp.
3. **2 to 3 mi. SE Glade.** Sec. 12 or 13, T. 5 S, R. 18 W, Phillips Co. FH No. 1650, *Saurodon* sp.
4. **Ransom.** Specimen probably from Trego Co. Pliocene exposures occur in vicinity of Ransom. FH No. 1652, *Ptychodus* sp.
5. **Purinton Ranch.** See Gove Co., Locality No. 16. FH No. 1659, *Protosphyraena* sp.
6. **7 mi. NW Ellis.** T. 12 S, R. 21 W, Trego Co. FH No. 1660, *Protosphyraena* sp.
7. **1½ mi. SE Elkader.** Sec. 11 or 12, T. 15 S, R. 32 W, Logan Co. FH No. 2024, *Protosphyraena* sp.
8. **N of Ogallah, Saline River.** E½ sec. 15, W½ sec. 14, T. 11 S, R. 22 W, Trego Co. FH No. 2025, *Protosphyraena* sp.
9. **5 mi. SW Gove City.** Central sections, T. 13 S, R. 29 W, Gove Co. FH No. 2081, *Isurus* sp.
10. **3¼ mi. SE Elkader.** Sec. 13 or 24, T. 15 S, R. 32 W, Logan Co. FH No. 2714, *Isurus* sp.
11. **3 mi. N of Bogue, N side of S Fork Solomon River.** Sec. 6, T. 8 S, R. 21 W, Graham Co. FH No. 5014, *Cimolichthys* sp.
12. **NW Bogue.** See FH Locality No. 11. FH No. 8395, *Xiphactinus* sp.
13. **S Brakes, Butte Creek, Logan Co.** Sec. 15 or 16 (according to Marion Bonner), T. 15 S, R. 34 W. FH No. 8567, *Ichthyodectes* sp.
14. **Marvin Albin Ranch about halfway between Castle Rock and Smoky Hill River.** ?sec. 24, T. 14 S, R. 26 W, Gove Co. FH No. 10688-288, *Ptychodus* sp.

Reptiles

15. **6 to 7 mi. SE Russell Springs.** T. 14 S, R. 34 W, Logan Co. FH No. 4, *Tylosaurus* sp.
16. **5 mi. NW Elkader.** T. 14 S, R. 32 W, Logan Co. FH No. 2085, *Pteranodon* sp.
17. **2 mi. NE Penokee.** Sec. 13, T. 8 S, R. 24 W, Graham Co. FH No. 2851, *Pteranodon* sp.
18. **Mendenhall Ranch, 4 mi. E Gove City.** Sections 16, 17, T. 13 S, R. 28 W, Gove Co. FH No. 2913, *Platecarpus* sp.
19. **Between Bogue and Hill City, 200 steps from the N side of the S Fork, Solomon River.** Sec. 12, T. 8 S, R. 22 W, Graham Co. FH No. 5426, *Pteranodon* sp.
20. **3 mi. NE Gove (City).** Sec. 32, T. 12 S, R. 28 W, Gove Co. FH No. 7109, *Tylosaurus* sp.
21. **Garrett Ranch.** See KU Trego Co., Locality No. 23. FH No. 7937, *Clidastes* sp.
22. **N Russell Springs.** See KU Logan Co., Locality No. 5. FH No. 7960, plesiosaur.
23. **About 1 mi. SW Russell Springs.** See KU Logan Co., Locality No. 5. FH No. 8400, *Toxochelys* sp.

24. **Horse Thief Canyon.** W½ sec. 9, T. 13 S, R. 26 W, Gove Co. FH No. 10560, *Pteranodon* sp.
25. **9 mi. NW Wakeeney, Garrett Ranch.** See KU Trego Co., Locality No. 23. FH No. 10598, *Pteranodon* sp.
26. **7 mi. W Gove City, Emerson Ranch.** ?sec. 36, T. 12 S, R. 30 W, Gove Co. FH No. 10856, mosasaur.
27. **Brakes of Hell Creek.** See KU Logan Co., Locality No. 23. FH No. 11311, *Nyctosaurus* sp.

American Museum of Natural History

Kansas Cretaceous vertebrates in the American Museum include the majority of type specimens from the chalk. Most of the material was gathered by E. D. Cope and his collectors in the 1870s. Specimens having locality records traceable to section, township and range are few. Localities from which specimens in the American Museum were obtained are cited in Cope (1875). Several localities described by Cope are in areas lacking exposures of chalk. Other localities described as in yellow chalk are actually in gray or black Pierre Shale (Adams, 1898). Several sites are close to stations of the Butterfield Overland Stage. Cope probably followed parts of the stage route, which closely approaches chalk exposures. He visited western Kansas in 1871. Starting from Fort Wallace (sec. 29, T. 13 S, R. 38 W) he went S and E exploring exposures in Logan County along the Smoky Hill River and Butte Creek. The localities from which he described specimens of reptiles and fishes are listed with page references to Cope (1875).

1. **S of Ft. Wallace on Butte Creek in the yellow chalk (p. 67).** Although the upper drainage of Butte Creek lies S of Ft. Wallace, exposures of yellow chalk do not appear until one enters Logan Co. in R. 37 W. The locality is uncertain.
2. **Smoky Hill River 5 mi. W Ft. Wallace in yellow limestone (p. 70).** Exposures W of Ft. Wallace are Pierre Shale. Small exposures of yellow chalk appear about 2 mi. SW of the Fort on the S side of the Smoky Hill River (sec. 32, T. 13 S, R. 38 W and sec. 5, T. 14 S, R. 38 W).
3. **Near mouth of N. branch of Smoky Hill River (p. 74).** Material from small exposures of the Niobrara Formation and/or Pierre Shale in the vicinity of Forks of the Smoky Hill River Stage Station, NE¼ T. 13 S, R. 36 W.
4. **Fossil Spring Canyon (p. 133, 144, 223).** Cope obtained several specimens from this locality. Unfortunately I have been unable to identify the site definitely. Cope refers (Osborn, 1931:163) to a spring 4 mi. beyond Twin Buttes. At this point (sec. 4, T. 15 S, R. 36 W) a small tributary of Butte Creek is 2 mi. or less from the south bluffs of Butte Creek where extensive chalk exposures are developed.
5. **Bluff of Butte Creek (p. 135).** Probably in the vicinity of Locality No. 4.
6. **6 mi. S Sheridan (p. 138).** Sheridan (W½ sec. 8, T. 12 S, R. 36 W) was a terminus of the Kansas Pacific (now Union Pacific) Railroad in 1870-71. Six miles S of Sheridan would place the locality along the N Fork of the Smoky Hill River where numerous exposures of Pierre Shale and one or two exposures of Smoky Hill Chalk are developed. Cope cites (p. 157) a specimen from the yellow chalk 6 mi. S of Sheridan.

7. **Fossil Spring Canyon near mouth of Fox Canyon (p. 144).** Cope (p. 18) described these canyons as follows: "Butte Creek valley, fifteen to eighteen miles to the south [presumably S of the Smoky Hill River], is margined by bluffs of from twenty to one hundred and fifty feet in height. . . . The bluffs of the upper portion of Butte Creek, Fox and Fossil Spring (five miles south [*sic*]) Cañons are of yellow chalk; and the reports of several persons stated that those of Beaver Creek, eight miles south of Fossil Spring, are exclusively of this material." This information is inadequate to locate these canyons. Butte Creek lies about 10 miles south of the Smoky Hill River. The locality of Fossil Spring is uncertain (see Locality No. 4). If Cope meant that Fossil Spring was five miles south of the Smoky Hill River, Fossil Spring would be in the flat valley of this river rather than in a canyon. Beaver Creek (now called Ladder Creek) is at least eight miles and most parts are 12 to 15 miles south of Butte Creek. Rocks of the Niobrara Formation are exposed only near the mouth of Ladder Creek.
8. **N bank, Smoky Hill River, 30 mi. E Ft. Wallace (p. 149).** This locality must lie in the south half of T. 13 S, R. 33 W along Twelve Mile Creek and in the vicinity of the Smoky Hill Stage Station (S½, E½ sec. 32, T. 13 S, R. 33 W).
9. **Fox Canyon S of Ft. Wallace (p. 149).** See AMNH locality Nos. 1 and 7.
10. **Gypsum Buttes (p. 150).** Cope stated that these buttes lie 1 mi. SW of Sheridan (see AMNH Locality No. 6) in sec. 13, T. 12 S, R. 37 W. Cope also refers to Twin Buttes near Butte Creek. Twin Buttes lie in sec. 1, T. 15 S, R. 37 W. There are several chalk exposures near Twin Buttes.
11. **1 mi. SE Sheridan on the North Fork of the Smoky Hill River (p. 157).** Sec. 8 or 17, T. 12 S, R. 31 W.
12. **Low bluff on Butte Creek, 14 mi. S of Ft. Wallace (p. 160).** Cope must have meant SE of the Fort. Exposures 14 mi. S of Ft. Wallace are beyond Butte Creek and in Tertiary rock. The locality cannot be determined.
13. **Fox Canyon near Ft. Wallace (p. 194).** See AMNH Locality No. 7.
14. **Solomon River 160 miles from junction with Kansas River (p. 201).** Near Hill City, Graham Co.
15. **Russel Spring on the Smoky Hill River (p. 209).** Near the Russel Spring Stage Station. The fossils probably came from the S½ T. 13 S, R. 35 W.
16. **15 mi. S Ft. Wallace (p. 217).** See AMNH Locality Nos. 1 and 12.
17. **Fossil Spring near Ft. Wallace (p. 223 and 225).** See AMNH Locality No. 7.
18. **Near Stockton (p. 244).** Stockton is in Rooks County. Numerous small exposures of chalk are developed near Stockton.
19. **Spring Creek, Rooks County (p. 244d).** Spring Creek flows north into the South Fork of the Solomon River in T. 8 and 9 S, R. 20 W.

The following are localities of specimens of fish in the American Museum from the Kansas Cretaceous collected prior to 1940.

20. **Sand Creek, 2 to 3 mi. and 5 mi. above S Fork Solomon River.** Sand Creek (T. 10 S, R. 19 and 20 W) lies in Rooks County and flows into the Saline River. AMNH Nos. 1705, 1706, and 2062.
21. **7 mi. SW Castle Rock, Trego Co.** See KU Gove Co., Locality No. 5. AMNH No. 1747.
22. **Upper Fox Creek.** ?Equals Fox Canyon. See AMNH Locality No. 7. AMNH No. 1915.
23. **T. 13 S, R. 24 W, Trego Co.** Exposures of the Niobrara Formation do not appear in this range and township. Possibly this locality should be T. 13 or 14 S, R. 25 W. AMNH No. 2003.

24. **2 mi. E Sugarloaf, T. 6 S, R. 19 W, Rooks Co.** This site is in sec. 12. AMNH No. 2307.
25. Uncatalogued specimens of "berycoids" are recorded from:
    a) **½ mi. S Castle Rock.** Sec. 1, T. 14 S, R. 26 W.
    b) **3 mi. SW Castle Rock.** See KU Gove Co., Locality No. 5.
    c) **2.5 mi. E Castle Rock.** See KU Trego Co., Locality No. 7.

PEABODY MUSEUM OF NATURAL HISTORY

Extensive collections of reptilian and fish material in the Peabody Museum bear little or no record of locality. O. C. Marsh obtained the majority of Kansas Cretaceous fossils now at the Peabody Museum through the efforts of his collectors, primarily B. F. Mudge. Marsh's main contribution to our knowledge of Kansas Cretaceous fossils appears in his monograph (1883) on the so-called toothed birds. Localities cited, in that work, which can be identified to section, township and range are indicated below.

1. **S bank Smoky Hill River about 20 mi. E of Ft. Wallace (p. 195).** Sec. 27, T. 13 S, R. 35 W. Near Russell Springs, Logan Co.
2. **12 mi. E Ft. Wallace (p. 195, 198).** Sec. 11 or 13, T. 13 S, R. 36 W. Near Forks of the Smoky Hill River Stage Station.
3. **Hackberry Creek, near Smoky Hill River, Gove Co. (p. 199).** Sec. 31, T. 13 S, R. 25 W. Specimens were probably from near the Castle Rock Creek Stage Station.

UNITED STATES NATIONAL MUSEUM

With the exception of the State College Museum collections at Fort Hays, the U. S. National Museum collections of Kansas Niobrara vertebrates are less numerous than those of other museums discussed above. Specimens collected by Dr. David Dunkle during the past 15 years bear adequate locality data. Material collected earlier by Mr. George Sternberg and others is cited below and section, township and range are indicated or reference is made to identical localities of the University of Kansas Museum of Natural History.

1. **10 mi. NW Wakeeney.** This mileage was probably overestimated. George Sternberg collected fossils in this area from the Garrett Ranch. See KU Trego Co., Locality No. 23. USNM No. 21081.
2. **Hackberry Creek, 3 mi. below Gove City.** See KU Gove Co., Locality No. 8. USNM No. 12061.
3. **12 mi. SE Russell Springs.** Sec. 16, T. 15 S, R. 34 W. This locality is called "Robber's Roost" by George Sternberg. This site is on land that was part of the Berry Farm, a name which appears on labels of some specimens. USNM No. 12358.
4. **25 mi. S of Oakley, S side of the Smoky Hill River.** T. 15 S, R. 35 W. USNM No. 11554.
5. **2½ mi. S and 2 mi. E Oakley.** Sec. 13 or 14, T. 15 S, R. 32 W. USNM No. 11650.
6. **14 mi. S Quinter.** Sec. 16, T. 13 S, R. 26 W. Andrew Bird Ranch. USNM No. 11557.
7. **5 mi. SE Russell Springs.** Sec. 6, T. 14 S, R. 34 W. USNM No. 18224.

Museum of Comparative Zoology, Harvard University

Many of the specimens at the Museum of Comparative Zoology are uncatalogued and locality records are scanty. St. John is a frequently-cited locality. Logan County originally bore the name St. John County. The specimen cited below is the only one having locality record adequate to determine section, township and range.

1. 4 mi. N of the Pyramids (Monument Rocks). ?sec. 18, T. 14 S, R. 31 W, Gove Co. MCZ No. 5400.

REMARKS

It is hoped that clarification of localities from which Kansas Niobrara Cretaceous vertebrates have been obtained will assist in future studies of these vertebrates. It would be premature to commence ecologic or stratigraphic investigations of Niobrara vertebrates from locality data alone. Intensive taxonomic study of each vertebrate group represented in the chalk is required because earlier workers unnecessarily multiplied the number of specific names. Modern anatomical and taxonomic studies of vertebrate fossils from the Niobrara Formation of Kansas are just beginning. Dale Russell is reviewing the mosasaurs; T. H. Eaton and D. Bardack are revising several families of fishes.

That geographic differences in the distribution of Kansas Niobrara Cretaceous vertebrates do exist is demonstrated by two groups of fishes. Teeth of the elasmobranch *Ptychodus* are confined to eastern exposures of the Niobrara Formation in Gove and Trego counties and have not been found in Logan County where western exposures of the Niobrara Formation in Kansas are developed. Specimens of *Protosphyraena* are more abundant in eastern than in western chalk beds. Thus, *Ptychodus* and *Protosphyraena* are found only in the eastern or stratigraphically lower levels of the Smoky Hill Chalk or at best are more numerous in these levels. Distributional differences among the reptiles may be more pronounced than among the fishes. This is suggested by Dale Russell (personal communication).

Collections of Niobrara Cretaceous vertebrates from Kansas come primarily from areas of numerous, broad exposures in the west-central part of the State. Northeastern exposures of the chalk have scarcely been examined. Efforts to collect specimens in such areas might produce new kinds or indicate ecologic or stratigraphic differences relative to the area of Kansas from which Cretaceous vertebrates are well known.

BIBLIOGRAPHY

ADAMS, G. I.
1898. The Upper Cretaceous of Kansas: A historical review. Univ. Geol. Surv. Kansas. 4:15-27.

COPE, E. D.
1875. The vertebrata of the Cretaceous formations on the West. Rept. U. S. Geol. Surv. Territ. 2:1-303.

HODSON, W. G.
1960. Geology and ground-water resources of Gove County, Kansas. Univ. Kansas Publ. State Geol. Surv. Bull. 145:1-126.
1963. Geology and ground-water resources of Wallace County, Kansas. Univ. Kansas Publ. State Geol. Surv. Bull. 161:1-108.
—— Geology and ground-water resources of Trego County, Kansas. Univ. Kansas Publ. State Geol. Surv. in press.

JOHNSON, C. R.
1958. Geology and ground-water resources of Logan County, Kansas. Univ. Kansas Publ. State Geol. Surv. Bull. 129:1-175.

OSBORN, H. F.
1931. Cope: Master Naturalist. Princeton Univ. Press, xvi + 740 pp.

PRESCOTT, G. C., JR.
1955. Geology and ground-water resources of Graham County, Kansas. Univ. Kansas Publ. State Geol. Surv. Bull. 110:1-98.

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Chorda Tympani Branch of the Facial Nerve In the Middle Ear of Tetrapods

BY

RICHARD C. FOX

University of Kansas
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Chorda Tympani Branch of the Facial Nerve In the Middle Ear of Tetrapods

BY

RICHARD C. FOX

In recent years the middle ear of tetrapods has received the attention of numerous morphologists in the attempt to clarify the histories of amphibians, reptiles and mammals. Some workers have been more concerned with the comparative anatomy of the middle ear among Recent tetrapods than with its morphology in fossil genera. It should be noted, however, that paleontological and neontological approaches have seldom been mutually exclusive. Students of the middle ear of tetrapods who have approached the subject from a phylogenetic standpoint usually have invoked accessory evidence provided by Recent amphibians, reptiles and mammals to support conclusions; similarly, students relying primarily upon the morphology of the middle ear in Recent tetrapods have used some evidence provided by fossils. Neither "school" has been entirely successful in revealing the events that occurred in the evolution of the middle ear in the major groups of tetrapods.

Both neontological and paleontological studies have failed to account satisfactorily for the position of the chorda tympani branch of the facial or seventh cranial nerve in relation to the stapes and its processes. The stapes of reptiles and their amphibian ancestors characteristically possesses three processes:

1. A dorsal process, usually ossified, that extends upward and makes contact with the paroccipital process of the opisthotic.
2. A tympanic process, usually cartilaginous, that extends outward and makes contact with the tympanum.
3. A quadrate process, usually cartilaginous or ligamentous, that makes contact with the quadrate.

In the embolomerous ancestors of reptiles the quadrate process is thought to have extended outward and downward from the stapes to the quadrate. Consequently, the long axes of the tympanic process and the quadrate process were in the same vertical plane. With the advent and evolution of reptiles, the stapes descended to a more ventral position in relation to the quadrate. The quadrate process, swinging upward approximately 90 degrees, extended outward and forward to the quadrate. The long axes of the tympanic process and quadrate process then lay in a horizontal plane. This stage in the evolution of the middle ear had already been achieved in primitive pelycosaurs and captorhinomorphs.

In Recent reptiles and birds the chorda tympani passes forward across the tympanic cavity in a path that is dorsal to the tympanic process of the stapes. Thereafter, the chorda tympani curves down below the quadrate process of the stapes and extends ventrally and anteriorly to the lower jaw. In Recent mammals, however, the position of the nerve relative to that of the stapes is indeterminate; the malleus and incus are interposed between the stapes and the tympanum. The nerve crosses the tympanum through the posterior malleolar folds, between the dorsal pars flaccida and the ventral pars tensa of the membrane. In frogs the nerve extends anteriorly across the tympanic cavity

beneath the stapes before descending to the lower jaw. The manner in which these differences are to be explained has resulted in controversy; the most recent and important attempts to resolve the seeming incompatibilities of the position of the nerve in the middle ear have been by Vaughn (1955) and Hotton (1960).

It is generally thought that the primitive position of the chorda tympani was post-tympanic; in the first amphibians the nerve presumably passed forward across the tympanic cavity beneath the tympanic attachment of the stapes. The anuran condition has been supposed to be a retention of the primitive relationship between the nerve and the stapes (see, for example, Hotton, 1960), although deBeer (1937) would ascribe the position of the nerve in frogs and toads to peculiarities in the development of the chondrocranium in those animals. Additional support for the post-tympanic course of the nerve has been provided by Hotton (1960), who has suggested that during the change of the rhipidistian hyomandibular to the tetrapod stapes the nerve was pushed forward by the quadrate process as the hyomandibular swung out from the anteroposterior rhipidistian orientation to the definitive transverse tetrapod orientation. To accomplish this, the nerve had to drape across the quadrate process of the stapes, and Hotton (1960) has suggested that it did so indeed.

The descent of the tympanum from its dorsal labyrinthodont position to its ventral position among primitive captorhinomorphs and synapsids has been recognized in the attempts of both Vaughn (1955) and Hotton (1960) to explain the new position of the chorda tympani still found in Recent diapsids and birds. Vaughn suggested that during the amphibian-reptilian transition, with descent of the tympanum, the chorda tympani rose from its passage below the stapes to a new passage above the stapes. The vehicle of transfer in this scheme was a hypothetically thick tympanum through which the chorda tympani passed distal to the termination of the stapes. As Hotton (1960) has pointed out, such events are dependent upon the nerve passing across the tympanic cavity in a path close enough to the tympanum during its descent to permit the membrane to "seize" the nerve. Hotton rightly questions the supposition of Vaughn that the nerve was unusually close to the tympanum in embolomeres; nor is there any evidence to suggest that the membrane was unusually thick in these reptilian ancestors.

Hotton's (1960) explanation of the change from a post-tympanic to pre-tympanic path followed by the chorda tympani during the embolomere-reptilian transition is more complex than that of Vaughn. Hotton believed, as noted above, that in the first amphibians the chorda tympani crossed the tympanic cavity by passing under the tympanic process and over the quadrate process of the stapes. With the loss of the otic notch of the embolomeres, the tympanic process underwent reduction and was finally lost as well. Concurrently with these changes, the quadrate process of the stapes became increasingly ossified. With reduction of the tympanic process and loss of the otic notch the tympanum achieved a ventral attachment to the quadrate process. The continued emphasis of the quadrate process, now the functional stapes, led to the cradling of the tympanum by the dorsal edge of the process. The chorda tympani still retained its primitive relationship to the quadrate process by crossing above the bone. The appearance of reptiles more advanced than those represented by *Dimetrodon*, such as *Captorhinus*, involved most importantly the development of a new tympanic process of the stapes. If this

neomorph arose distal to the path of the chorda tympani the relation of the nerve to the stapes found in living diapsids was achieved; if the neomorph arose proximal to the path of the nerve, the nerve and stapes were related in a fashion that explains the appearance of the mammalian condition.

There is, however, considerable evidence that these events did not occur. In no living tetrapod known to me does the chorda tympani pass *above* or *loop over* the quadrate process of the stapes prior to the descent of the nerve to the lower jaw. For example, in *Lacerta* and *Ctenosaura* the chorda tympani passes below the stapedial-quadrate articulation (Goodrich, 1930; Oelrich, 1956); this relationship of nerve to articulation is also present in *Gecko* (deBeer, 1937). Similarly, the developmental history of mammals reveals that the path of the chorda tympani is external to the stapedial-incus articulation; the passage of the chorda tympani across the medial face of the mammalian tympanum corroborates this. Nor is there any phylogenetic necessity for supposing that the chorda tympani passed dorsal to the quadrate process in the history of tetrapods. During the change of the rhipidistian hyomandibular to the tetrapod stapes, the hyomandibular branch of the seventh nerve, arising from a common root with the chorda tympani, remained in back of the quadrate process as the hyomandibular swung out to achieve its tetrapod orientation. I suggest that the chorda tympani also remained behind the hyomandibular while this change was taking place, allowing the nerve to run forward beneath both the tympanic and quadrate processes of the stapes.

There is no evidence to suggest that the quadrate process of the stapes in primitive reptiles became heavily ossified and performed as a functional stapes. Indeed, Romer and Price (1940) refer to obvious scars on the ventral surface of the stapes and a pit on the medial face of the quadrate in *Dimetrodon*. They suggest that the scars and pit served as the proximal and distal attachments, respectively, of a typically ligamentous or cartilagenous quadrate process.

Both Vaughn's (1955) and Hotton's (1960) approaches are handicapped by the limitations that are inherent in forcing the features of adult morphology into a phylogenetic scheme that is itself a recitation of the history of adult animals. Both workers presuppose spatial barriers (the stapes and its processes) to the change in the path of the chorda tympani that may not have been present ontogenetically at the time that the nerve changed from a posttympanic position to a pretympanic position. The descent of the tympanum from the dorsal position that it occupied in the adult embolomeres was paralleled presumably by the descent of the tympanic diverticulum in the embryos of those animals involved in the amphibian-reptilian transition. The more ventral position of the tympanic diverticulum probably blocked the chorda tympani as it pursued its primitive course across the floor of the developing tympanic cavity. Freedom for the nerve's path was then found dorsal to the cavity. The subsequent appearance of the stapes was consequently ventral to the nerve. This ontogenetic sequence of the nerve and tympanic diverticulum is known among amniotes; it occurs, for example, in the developing chick (Patten, 1951).

In the manner described above, the position of the chorda tympani in mammals is easily derived from the pretympanic position of the nerve in primitive reptiles. The events that have just been discussed presumably obtained in both primitive captorhinomorphs, ancestral to living diapsid rep-

tiles, and primitive pelycosaurs, ultimately ancestral to mammals. In primitive pelycosaurs the quadrate was quite deep; the stapes extended posteroventrally towards the quadrate. The chorda tympani passed over the tympanic process and under the quadrate process, both of which were developed to a degree that was generally characteristic of early reptiles. The dorsal process of the stapes arose close to the footplate, in a proximal position on the stapedial rod.

The stapes of therapsids differed in several respects from the stapes of pelycosaurs. The bone was much smaller than in pelycosaurs; the reduction seems to have been most extreme in quadrate and tympanic processes. *Thrinaxodon* (Estes, 1961), *Kingoria* (Cox, 1959), and *Placerias* (Camp and Welles, 1956), for example, show the distal termination of the bony stapes to be close to the quadrate and thus close to the plane of the tympanum. Additionally, in these animals the dorsal process had lost the proximal position it had possessed among pelycosaurs and arose far out along the stapedial rod, close to its distal termination. The consequence of the new position of the dorsal process was a restriction of the space between the dorsal process and the tympanum through which the chorda tympani passed; what had been a wide channel dorsal to the stapes for passage of the chorda tympani was now a narrow slit. Continued decrease of this space through which the chorda tympani passed probably brought the nerve into contact with the tympanic membrane; in its passage above the stapes the nerve was trapped by the tympanum.

At this point, however, the chorda tympani still maintained its position ventral to the attachment between the stapes and the quadrate. It should be noted also that the articulation between the quadrate and the articular was lateral to the passage of the nerve. The migration of the quadrate and articular into the middle ear consequently followed a path that moved up and over the chorda tympani, completely free spatially from the passage of the nerve and in no way altering it.

The speed with which these later changes occurred in the mammalian-reptilian transition must have been comparatively great. No known fossils exhibit the intermediate stages between the achievement of a double articulation of the jaw and the incorporation in typical mammalian fashion of the quadrate and articular bones into the mechanism of the middle ear. But the explanation of the above changes requires no reliance upon macroevolutionary phenomena. The rate of change undoubtedly quickened, but the magnitude of the single changes need not be thought of as extraordinary.

As Hotton (1960) has noted, the captorhinomorphs and synapsids have given rise to all living mammals and reptiles, with the possible exception of turtles. The unified theory to explain the path of the chorda tympani in the higher classes of vertebrates supports Hotton's estimate of the ultimate origins of these groups, and argues against the classic sauropsid-theropsid dichotomy of living reptiles and mammals advocated by, among others, Goodrich (1930). The ancestry of turtles is obscure, in spite of the suggestion by Olson (1947) that they may be descended from diadectids. In turtles the chorda tympani is pretympanic. In diadectids the dorsal otic notch is retained, implying a retention of the embolomerous post-tympanic path of the chorda tympani. If turtles were derived from diadectids, the pretympanic path of the chorda tympani must have been achieved independently from all other living reptiles.

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LITERATURE CITED

Camp, C. L. and Welles, S. P.
1956. Triassic dicynodont reptiles. Mem. Univ. California, 13(4):255-348, 62 figs., 4 pls.

Cox, C. B.
1959. On the anatomy of a new dicynodont genus with evidence of the position of the tympanum. Proc. Zool. Soc. London, 132(3):321-367, 17 figs.

deBeer, G. R.
1937. The development of the vertebrate skull. Clarendon Press, Oxford. xxiii + 552 pp., 143 pls.

Estes, R.
1961. Cranial anatomy of the cynodont reptile *Thrinaxodon liorhinus*. Bull. Mus. Comp. Zool., 125(6):165-180, 3 figs., 2 pls.

Goodrich, E. S.
1930. Studies on the structure and development of vertebrates. Constable, London. xxx + 837 pp., 754 figs.

Hotton, N., III.
1960. The chorda tympani and middle ear as guides to origin and divergence of reptiles. Evolution, 14(2):194-211, 4 figs.

Oelrich, T. M.
1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). Misc. Publ. Mus. Zool., Univ. Mich., No. 94, 122 pp., 59 figs.

Olson, E. C.
1947. The family Diadectidae and its bearing on the classification of reptiles. Fieldiana: Geology, 11(1):2-53.

Patten, B. M.
1951. Early embryology of the chick. McGraw-Hill, New York. xiv + 244 pp., 102 figs.

Romer, A. S. and Price, L. I.
1940. Review of the Pelycosauria. Geol. Soc. Amer. Special Papers, No. 28, x + 538 pp., 71 figs., 46 pls.

Vaughn, P. P.
1955. The Permian reptile *Araeoscelis* restudied. Bull. Mus. Comp. Zool., 113(5):305-467, 15 figs., 2 pls.

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Fishes of the Kansas River System in Relation to Zoogeography of the Great Plains

BY

ARTIE L. METCALF

University of Kansas
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INTRODUCTION

Aims of this report are to (1) ascertain which species occur, (2) ascertain distributional patterns of the species and relate these to environmental conditions, and (3) relate the findings to the history and development of the Basin, and to the general zoogeography of fishes of the Great Plains and western part of the Interior Lowlands.

General Physical Features of the Kansas River System

Streams of the Kansas (or Kaw) River System arise in eastern Colorado and flow generally in an eastward direction, the mainstream debouching into the Missouri River at Kansas City (Figs. 1 and 2). Linearly, from west to east, the system traverses approximately 480 miles; the drainage area comprises 61,440 square miles.

The Kansas River proper is formed at Junction City, Kansas, by union of its two largest tributaries, the Smoky Hill and Republican rivers. The Smoky Hill River heads in Cheyenne and Kit Carson counties, Colorado, but tributaries in Colorado are highly intermittent at present. In western Kansas, the mainstream receives a few permanently flowing tributaries. From Wallace County, Kansas, east to Lindsborg, Kansas, the Smoky Hill River maintains a fairly straight eastward course. Near Lindsborg the Smoky Hill River turns sharply northward (probably the result of a stream-capture to be discussed later). Near Salina it acquires its two longest tributaries—the Saline and Solomon rivers. The Saline River, one of the saltiest streams in the United States according to Parker (1911:220), flows a linear distance of approximately 220 miles almost due east. The Solomon River, which is slightly longer than the Saline, consists of two parallel-flowing branches, North Fork and South Fork.

The Republican River heads in eastern Colorado where it, unlike the Smoky Hill River, possesses a number of permanently flowing tributaries. The Republican River proper is formed by confluence of its North and South forks and of the Arikaree River in Dundy County, Nebraska. For approximately 225 miles (linearly) the mainstream of the Republican River flows parallel to and slightly north of the Kansas-Nebraska border. From the northwest the Republican River receives Frenchman Creek, Red Willow Creek,

Medicine Creek and numerous shorter tributaries. Major southwestern tributaries are Beaver, Sappa and Prairie Dog creeks, all parallel-trending streams that head in northwestern Kansas. In Nuckolls County, Nebraska, the Republican River turns sharply southward into Kansas, then southeastward to Junction City. Few tributaries enter the Republican River in Kansas other than White Rock Creek, which joins the Republican in Republic County.

Near Manhattan, Kansas, the Kansas River receives another major tributary from the north—the Blue River, having an impoundment, Tuttle Creek Reservoir, north of Manhattan.

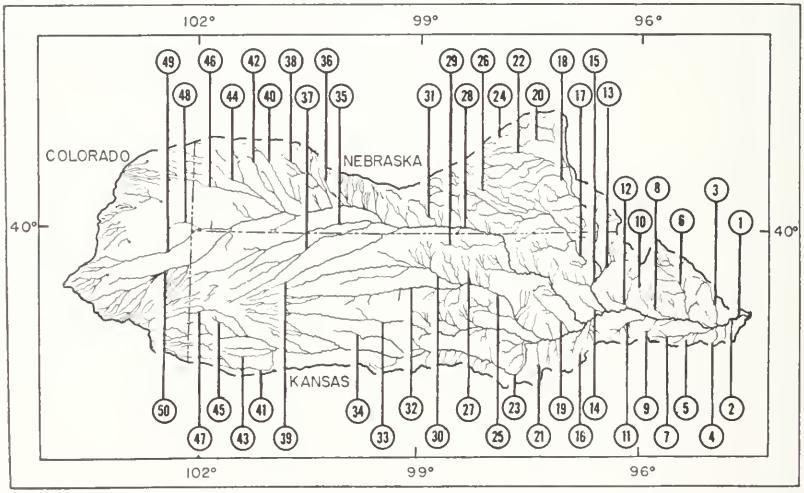

Fig. 1. Major streams of the Kansas River Basin. Names of streams to which numbers refer are indicated in Table 1. (Scale as in Figure 2).

Table 1. Noteworthy Streams of the Kansas River Basin. Numbers Are on Fig. 1 and the Streams to Which They Refer.

1. Kansas River
2. Mill Creek
3. Stranger Creek
4. Captain Creek
5. Washington Creek
6. Delaware River
7. Wakarusa River
8. Soldier Creek
9. Mission Creek
10. Cross Creek
11. Mill Creek
12. Vermillion River
13. Black Vermillion River
14. Wildcat Creek
15. Big Blue River
16. Lyon Creek
17. Little Blue River
18. Turkey Creek
19. Chapman Creek
20. Lincoln Creek
21. Gypsum Creek
22. Beaver Creek
23. Smoky Hill River
24. Big Blue River
25. Solomon River
26. Big Sandy Creek
27. Limestone Creek
28. Republican River
29. White Rock Creek
30. North Fork Solomon River
31. Thompson Creek
32. South Fork Solomon River

33. Saline River
34. Big Creek
35. Beaver Creek
36. Deer Creek
37. Sappa Creek
38. Medicine Creek
39. Prairie Dog Creek
40. Red Willow Creek
41. Ladder Creek
42. Blackwood Creek
43. Chalk Creek
44. Spring Creek (trib. of Stinking Water Creek)
45. Turtle Creek
46. Frenchman Creek
47. North Fork Smoky Hill River
48. Arikaree River
49. North Fork Republican River
50. South Fork Republican River

East of Manhattan the major northern tributaries of the Kansas River are the Vermillion River, the Delaware River and Stranger Creek; major southern tributaries are Mill Creek and the Wakarusa River. Along its lower course the Kansas River proper has not been impounded, although there is a low dam at Lawrence.

PHYSIOGRAPHY, GEOLOGY AND THE FAUNA

The landscape of the Kansas River Basin is mostly a product of Pleistocene and Recent geomorphic activity, although large expanses of only slightly modified Pliocene surface features exist in

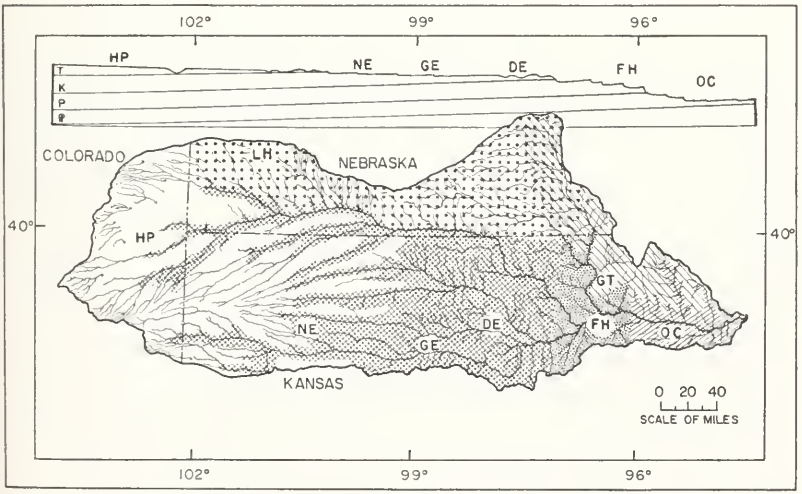

FIG. 2. Important physiographic and geologic features of the Kansas River Basin bearing on the distribution of fishes. Above is a highly generalized cross-section (west-east) across the central part of the Basin in northern Kansas and eastern Colorado: T = Tertiary; K = Cretaceous; P = Permian; ¶ = Pennsylvanian.
Below certain physiographic areas are indicated: HP = High Plains; NE = Escarpment formed on the Niobara Formation or Chalk Hills; GE = Escarpment formed on the Greenhorn Limestone Formation or Kearney Hills; DE = Escarpment formed on the Dakota Formation or Smoky Hills; FH = Flint Hills; OC = Osage Cuestas; LH = Loess Plains or Loess Hills; GT = Glacial Till-plains—NE, GE, and DE are all Cretaceous in age.

the western part of the basin. All of the major glacial advances known to have developed in northeastern North America have left traces of their influence in the Basin, but ice of only two major glaciations, the Nebraskan and the Kansan, is thought actually to have reached the present confines of the Basin (Frye and Leonard, 1952:58).

Glacial Till-Plains

In Kansas, glacial till associated with the advance of Nebraskan ice has been identified with certainty only in the extreme northeastern corner of the state where it is covered by till deposited during the subsequent Kansas Glaciation (Frye and Leonard, 1952:57). Lugn (1935:40) indicated that, in eastern Nebraska, Nebraskan till is characteristically thicker than Kansan till. Nevertheless, where not masked by Kansan till, the Nebraskan till has been eroded and covered by various sediments, chiefly glacial outwash and loess, to such an extent that the till is of little consequence in a consideration of present physiography.

Glacial till of Kansan age is, on the other hand, an important physiographic feature (Fig. 2). Kansan glacial till is found as far west as Marshall and Washington counties and as far south as central Wabaunsee, Shawnee and Douglas counties (Frye and Leonard, 1952:76, 77; O'Connor, 1960:50-52). In the southern part of the Big Blue River Drainage in Nebraska, Lugn (1935:Pl. 1, 68, 69) indicated the presence of Kansan till as far west as Fillmore and Jefferson counties, extending approximately to the valley of the Little Blue River. North of Crete, Nebraska, Lugn was not able to discern Kansan till west of Seward and Butler counties. Delimitation of the boundaries of the till area is difficult due to the large amount of dissection that has occurred around the periphery of the till sheet. Erosion probably was facilitated by thinning of the original till sheet toward its margins. Factors other than erosion that have modified the Kansan till sheet since its deposition are soil-formation and further deposition, chiefly of loess, upon the till sheet. In a small area in the upper Big Blue River Basin in Nebraska thick loess overlies glacial till (Fig. 2). Several streams have headwaters in the Till Plains: the Big Blue River in Nebraska, the Black Vermillion River, the Vermillion River, the Delaware River and Big Stranger Creek. The lower parts of all these streams and lesser tributaries entering the Kansas River from the north have cut completely through the till mantle. After removal of the mantle some streams (especially in the area where

till covered the Shawnee Escarpment, discussed hereafter) have cut significant erosional valleys in the underlying bedrock (for example, Mud Creek, Nine-mile Creek and Wildhorse Creek). Above the point where these streams cut through the mantle to bedrock they have low gradient, bottoms of silt and sand and steeply-incised banks. Water is characteristically turbid. Below the point where these creeks cut through the till-mantle, water may remain turbid but gravel and rubble are common in stream-beds, gradient increases and rubbly riffles are formed. Concommitant with these physical changes are faunal changes. At seven collection-stations in the upper parts of the Delaware River and Big Stranger Creek above the point where glacial till is breached, only these species were found: *Semotilus atromaculatus, Notropis l. lutrensis, Notropis stramineus missuriensis, Phenacobius mirabilis, Pimephales promelas, Campostoma anomalum pullum* and *Ictalurus melas.* Below the breach in the till-mantle, the fauna is more diverse, including, in addition to the above species, *Pimephales notatus, Notropis cornutus, Catostomus commersoni, Ictalurus natalis, Lepomis cyanellus* and *Etheostoma spectabile pulchellum.*

Osage Cuestas

The Osage Cuestas (Fig. 2) are formed on Upper Pennsylvanian strata that dip slightly to the west. The rocks are sedimentary, deposited in cyclothemic manner (Moore, 1949:25). Limestones and shales predominate but some sandstones are present, especially in the Douglas Group. Drainage is to the east, opposite to the direction of dip, resulting in east-facing cuesta-scarps formed on the more resistant strata. Such scarps are best developed where thick, resistant limestone beds overlie thick, nonresistant shales, as in the Oread Limestone over the Lawrence Shale; some scarps are at least 200 feet high (Schoewe, 1949:284). From east to west several escarpments are definable.

Kansas City and Lansing Groups

Of the Kansas City and Lansing groups of the Missourian Series, the Wyandotte, Plattsburg and Stanton limestones contribute to the formation of steep scarps along Kill Creek, Cedar Creek and Mill Creek in Johnson County, Kansas, and along Kaw Creek, Wolf Creek and several other short tributaries north of the Kansas River in Wyandotte and southeastern Leavenworth counties. These streams generally have permanent flow of clear water and have

rubble bottoms and high gradients. The steep hillsides of their valleys have discouraged cultivation. Several species that are indicative of "good" (clear, unpolluted) water in the Kansas River Basin (*Notropis cornutus, Etheostoma spectabile pulchellum* and the crayfish *Orconectes luteus*) are found in these streams. Cedar Creek contains the most diverse fauna in this area. Mill Creek and small tributaries north of the Kansas River in Wyandotte County seem to have suffered some modification due to encroaching urban and industrial areas.

Douglas Lowlands

The Douglas Group of Pennsylvanian rocks is comprised largely of sandstone and shales. In northern Kansas these beds are weak, typically forming an area of low relief (herein termed "Douglas Lowlands"). Moore (1949:127) stated, "The outcrop belt of Douglas rocks is generally a rolling plain, bounded on the west by the east-facing Oread limestone escarpment. . . ." The watersheds of Little Wakarusa River, Spring Creek and Cole Creek are underlain, for the most part, by rocks of the Douglas Group. The Lawrence Shale Formation is the uppermost of the beds of the Douglas Group and forms the steep, continuous slope of the Oread Escarpment. Streams possess low gradients, silty or sandy bottoms, and water is characteristically turbid.

Shawnee Escarpments

The Shawnee Group, of which the Oread Limestone is the lowest formation, includes four scarp-forming limestones, the Oread, Lecompton, Deer Creek and Topeka (herein termed "Shawnee Escarpments"). Moore (1949:139, 141) in discussing the Shawnee outcrop belt noted, "It is distinguished from the Douglas and Wabaunsee belts by the greater prominence of escarpments and generally more rugged topography . . . In the vicinity of the Kansas River Valley, each of the Shawnee limestone formations makes a well-defined escarpment. . . ."

The Oread Escarpment is one of the best-defined of the upper Pennsylvanian escarpments in northern Kansas, and is especially prominent in the vicinity of Lawrence (reliefs in excess of 100 feet are common). Limestones of the Shawnee Group form escarpments, not only along the Kansas River proper but also around the margins of the erosional valleys of the Wakarusa River and its tributaries in the western half of Douglas County and in eastern

Shawnee County. North of the Kansas River, limestones of the Oread Formation form similar rims around the valleys of Mud Creek, Wildhorse Creek, Nine-mile Creek, and the middle part of the Big Stranger Creek System.

Wabaunsee Group

Escarpments of the Wabaunsee Group of the Virgilian Series are less impressive than those of the Shawnee Group. Topographically the area of outcrop in northern Kansas is predominantly a grassy, rolling upland. In its western part it is transitional to the Flint Hills in vegetation and topography. In this western part escarpments are formed by the Burlingame and Tarkio limestones. The watersheds of Snokomo, Mission and Soldier creeks are, for the most part, underlain by rocks of Wabaunsee age. The fish-fauna, as well as the flora, shows affinities to that of the Flint Hills directly to the west. *Notropis rubellus,* otherwise known only from the Flint Hills, was reported by Gilbert (1886:208) from Mission Creek (as *N. rubrifrons*).

Fauna of Wakarusa River

The Wakarusa River traverses terrain formed mainly on rocks of the Wabaunsee, Shawnee and Douglas groups. The kinds of fishes found in Wakarusa tributaries of approximately the same size, originating in these three areas of outcrop are discussed below. Eight species, most of them widespread in the Kansas River Basin, were taken at stations in all three sections of the watershed: *Semotilus atromaculatus, Notropis l. lutrensis, N. stramineus missuriensis, Pimephales promelas, P. notatus, Ictalurus melas, Lepomis cyanellus* and *L. humilis.* Other species taken in the three areas are listed in Table 2.

The lowest number of species (13) is from the Douglas Lowlands. The low relief developed on shales of the Douglas Group has made possible intensive cultivation of the area. Furthermore, the watershed of Little Wakarusa Creek, east of its channel, drains a surface of exceedingly low relief formed, according to O'Connor (1960:55), on deposits of Kansan glacial till and outwash.

In the survey by Deacon and Metcalf (1961) made in 1959, no orange-throated darters (*Etheostoma spectabile pulchellum*) were taken in streams on the Douglas Lowland. In June, 1963, this species was common at some stations on Little Wakarusa River and Cole Creek in this area. Deacon and Metcalf (1961:320)

Table 2.—Fishes Taken in Three Sub-divisions of the Wakarusa River Basin.

	Douglas group lowland	Shawnee group escarpments	Wabaunsee group upland
Carpiodes carpio		X	X
Catostomus commersoni		X	X
Notemigonus crysoleucas			X
Hybopsis biguttata		X	
Notropis umbratilis		X	X
Notropis cornutus		X	
Notropis topeka		X	
Phenacobius mirabilis	X	X	
Hybognathus placitus	X		
Campostoma anomalum	X	X	
Ictalurus punctatus	X	X	
Ictalurus natalis		X	
Pylodictis olivaris		X	
Noturus flavus		X	
Noturus exilis		X	
Percina caprodes		X	X
Etheostoma nigrum		X	
Etheostoma spectabile	X	X	
Micropterus salmoides		X	X
Lepomis macrochirus		X	X
Lepomis megalotis		X	

theorized that *E. s. pulchellum* had been extirpated in much of the Wakarusa River System by drought in 1952-1956 and that in 1959 it had not, due to a slow rate of dispersal, repopulated much of the Basin from its refugia in streams draining the Oread Escarpment, but by 1963 had dispersed to intermittent—less favorable but temporarily habitable—streams of the Douglas Lowlands.

In the area of the Shawnee Escarpments 27 species were recorded—more than twice the number found on the plain formed on rocks of the Douglas Group. Ten species were found exclusively in the zone of Shawnee Escarpments. On the upland plain formed on rocks of the Wabaunsee Group 15 species were collected, none exclusively in that part of the Wakarusa Basin.

Flint Hills

West of the Osage Cuestas the Kansas River traverses the Flint Hills, cuesta-scarps formed on limestones of Lower Permian age (Gearyan) (Fig. 2). Major southern tributaries are (east to west) Mill Creek, Antelope Creek, Deep Creek, McDowell Creek, Clarks Creek and Lyon Creek. From the north the Kansas River receives (east to west) Cross Creek, the Vermillion River, the Blue River,

Wildcat Creek, Seven Mile Creek and Three Mile Creek. Much of the watershed of the Vermillion River is underlain by rocks of Pennsylvanian age (Wabaunsee Group) because of the presence of the buried Nemaha Mountains which have brought these deeper-lying rock strata to the surface in Pottawatomie and Nemaha counties in Kansas and in Pawnee and Richardson counties and northward in Nebraska.

The cuestas of the Flint Hills generally possess greater relief than the Osage Cuestas because of the presence of thick beds of erosible shales separated at long intervals by especially resistant, often cherty limestones. The limestones are few in number. The Foraker, Grenola, Cottonwood, Wreford and Barneston formations are the principal scarp-makers.

Streams originating in the Flint Hills have high gradients. In the process of degradation large quantities of limestone and shale rubble and gravel have been stripped away and transported by streams, this forming the dominant type of stream-bottom. Distance of transport is seldom great enough to reduce the sediments to the size of sand or less. The sharp relief of the escarpments and rockiness of the soil have hindered cultivation, while the luxuriant growth of tall prairie grasses has encouraged ranching. Lack of cultivation makes for less turbid streams, and the native grasses inhibit runoff, which also enhances clarity of the water and permanency of the streams. Streams of the Flint Hills support the most diverse fauna of the entire Kansas River Basin. Minckley (1959) in a survey of the Blue River in Kansas, a watershed situated almost entirely within the Flint Hills, recorded a total of 53 species of fishes. This compares favorably with the total of 83 species recorded here for the entire basin of the Kansas River. Fishes common in upland tributaries of the Blue River are *Chrosomus erythrogaster, Semotilus atromaculatus, Pimephales notatus, Pimephales promelas, Notropis cornutus, Catostomus commersoni, Ictalurus melas, Ictalurus natalis, Etheostoma nigrum, Etheostoma spectabile pulchellum, Lepomis humilis,* and *Lepomis cyanellus.*

The clear streams of the Flint Hills, together with those draining the area of the Oread and other escarpments of the Shawnee Group, mentioned earlier, seem to have served as refugia for some species of fish and a crayfish that were formerly distributed more widely in the Kansas River Basin. Species that are still known to exist in both these refugia are *Notropis topeka, Noturus exilis, Etheostoma n. nigrum, Percina caprodes* and *Lepomis megalotis.* In recent

years *Hybopsis biguttata* has been taken only from Mill Creek in the Flint Hills of Wabaunsee County but it was found as late as 1924 in Rock Creek, Douglas County, in the area of the Oread Escarpment.

Four species are, at present, known only from the Flint Hills segment of the Basin. These are *Chrosomus erythrogaster, Notropis rubellus, Moxostoma erythrurum* and *Percina maculata. Moxostoma erythrurum* has been reported only from Mill Creek in Wabaunsee County, and recent records of *N. rubellus* are only from Mill Creek, where it flourishes, and from one locality in the Blue River Drainage.

In literature of the 1800's *Notropis hudsonius, Etheostoma blennioides* and *Percopsis omiscomaycus* were reported from the general area of the Flint Hills.

Of the species mentioned in the preceding three paragraphs *Chrosomus erythrogaster, Hybopsis biguttata, Notropis topeka* and *Etheostoma n. nigrum* were recorded in the 1800's from localities west of the Flint Hills. Recent changes in the distribution of *N. topeka* in the Kansas River System have been discussed by Minckley and Cross (1959).

Great Plains

All of the Kansas River Basin west of the Flint Hills is within the Great Plains Physiographic Province of Fenneman (1931). Indispensable to aquatic life in this vast, semiarid region is the presence of water-bearing sediments to furnish water for permanent stream flow. There are few such strata, the most notable ones being (1) the Dakota Formation, (2) certain Pleistocene sands and gravels, widespread in southern Nebraska and scattered elsewhere, (3) the Pliocene Ogallala Formation where it is exposed in contact with the underlying aquicluding Niobrara Formation or Pierre Formation both of Cretaceous age and (4) valley alluvium. The groundwater resources of the area are well known due to extensive work by the Kansas Geological Survey (reported mainly in Bulletins of the Kansas Geological Survey) and by the United States Geological Survey in Nebraska (reported in various USGS Water Supply Papers).

Dissected High Plains

The eastern edge of the Great Plains in Kansas is an area of rolling hills that has been treated variously by physiographers. Fenneman

(1931:25) termed this region the Plains Border, recognizing it as an area formerly part of the High Plains, but in the process of being degraded to a lower base level. Emphasizing this process of degradation, Schoewe (1949:302) employed the name "Dissected High Plains" for this region. The boundary between the Flint Hills and the Dissected High Plains is ill-defined, mainly due to the presence of an intervening plain formed on rocks of the Wellington Formation of Middle Permian age. The bedrocks of the Dissected High Plains continue northward into Nebraska but north of the Republican River are covered by loess, glacial till or both. It seems best to consider the Republican River as the northern boundary of the Dissected High Plains Physiographic District, including the area to the north in the Loess Plains District (Fig. 2).

The plain of the Wellington Formation in the Kansas River Watershed ranges in width from approximately 10 miles in Washington and Marshall counties to 35 miles in southern Dickinson and southeastern Saline counties. The principal tributaries of the Kansas River in this area are Holland and Turkey creeks from the south and Mud and Chapman creeks from the north. The Smoky Hill River here lacks the high bluffs characteristic of its erosional valley in the Flint Hills and Osage Cuestas to the east. According to Latta (1949:20) the Smoky Hill Valley is three to four miles wide where bordered by beds of the soft Wellington Shale but narrows to one to two miles after entering the area of outcrop of the more resistant limestones of Gearyan (Wolfcampian) age below Chapman in Dickinson County. The gradient of streams in this area is low; streams are turbid and have muddy bottoms. Bayne, Walters and Plummer (1959:57) characterized the Wellington Formation as a poor aquifer because of its low permeability. Presumably it yields little water to streams of the area. The fish-fauna is impoverished, especially as compared to that of the Flint Hills immediately to the east. Hassler (Unpublished dissertation, Kansas State University, 1940) surveyed the fishes of Chapman Creek in Clay and Dickinson counties. He reported only 11 species; these I interpret to have been *Lepisosteus osseus, Carpiodes c. carpio, Semotilus atromaculatus, Notropis stramineus missuriensis* (reported by Hassler as *N. cornutus*—possibly more than one *Notropis* was represented but *N. stramineus* surely was the most abundant species present), *N. lutrensis, Pimephales promelas, Campostoma anomalum pullum, Ictalurus melas, I. punctatus, Lepomis cyanellus* and *L. humilis* (listed by Hassler as *Eupomotis gibbosus*).

My collections in Holland, Mud, and Turkey creeks have revealed a similar paucity of species and have not added any species to the list given from Chapman Creek.

West of the plain formed on the Wellington Formation are three belts of hills in the Dissected High Plains District; the easternmost is commonly called the Smoky Hills, and the westernmost two comprise the Blue Hills (Schoewe, 1949:310).

The highly irregular escarpment of the Smoky Hills has developed on resistant beds of the Dakota Formation (DE in Fig. 2). The line of outcrop of this formation trends southwest to northeast, outcropping over large parts of Ellsworth, Lincoln, Ottawa, Cloud, and Washington counties (Schoewe, 1952:Fig. 1). Plummer and Romary (1942:327) described the Dakota Formation as consisting mostly of varicolored clays that include lenticular siltstones and channel sandstones that may appear at any stratigraphic level in the formation. These lenses are the most salient features of the formation topographically as they form the crests of the Smoky Hills.

In addition to its importance as a scarp-maker the Dakota Formation is noteworthy for its role as an aquifer in north-central Kansas (Fishel *et al,* 1948:82 Republic County and northern Cloud County; Berry and Drumm, 1952:25 Lincoln County; Hodson, 1959:66 Mitchell County). Water from this formation is variable in hardness. In Mitchell County, Hodson (1959:Table 5) found total hardness ranging from 27 ppm. to 816 ppm. and dissolved calcium from 7.1 to 296 ppm.

Where the Dakota Formation crops out, stream-flow is more nearly permanent than in the Wellington Plain to the east or the Blue Hills to the west.

The Blue Hills consist of two belts of hills, trending southwest to northeast. The easternmost escarpment is formed on the Greenhorn Limestone (GE in Fig. 2); the western escarpment, also called Chalk Bluffs, is formed on the Niobrara Chalk Formation (NE in Fig. 2). The Dakota Escarpment is separated from that formed on the Greenhorn Limestone by an area of little relief formed on the Graneros Shale; another such area that has formed on the Carlile Shale separates the Greenhorn Escarpment from that formed on the Niobrara Chalk. All of these rocks of the Blue Hills are poor aquifers. Ground water studies in the counties in which the Graneros Shale and Carlile Shale crop out, consistently report that few or no wells obtain water from these formations. The aquatic life of streams originating in the area of the Greenhorn Limestone

Escarpment is meager. The only streams of consequence are those that originate to the west and flow through the escarpment such as the Smoky Hill, Saline, and Solomon. Tributaries are shallow, generally intermittent, and most have silty bottoms.

The westernmost of the three escarpments of the Dissected High Plains, that formed on the Niobrara Chalk Formation (comprising the Fort Hays and Smoky Hill chalk members), does not form strong cuestas as do the other two but tends, rather, to produce the well-known and often bizarre bluffs, pinnacles and buttes of the "Chalk Bluffs" of western Kansas. In the Ladder Creek Drainage of Wallace, Greeley, Wichita, Logan, Scott, Gove, and Lane counties, Bradley *et al* (1957:16, 20) found that the Niobrara Formation was not an important aquifer but that it supplied water to a few wells in areas where no other water-bearing rocks were accessible. Hodson and Wahl (1960:64, 65) noted that "The Fort Hays Chalk Member is not known to yield water to wells in Gove County . . ." and that "The Smoky Hill Chalk Member is a poor aquifer in Kansas and yields very little water to wells in Gove County."

Streams draining the area of the Chalk Bluffs are highly intermittent. Twin Butte Creek and Chalk Creek in southern Logan County are streams 30 to 35 miles in length that, as their names suggest, traverse an area dominated by the Niobrara Chalk and the overlying Pierre Shale. Johnson (1958:17) reported that springs occur on Chalk Creek where its erosional valley is incised below the contact of the Ogallala and Niobrara formations. He reported springs as common in one central part of the stream but added that "running water in the channel farther downstream is infrequent during the hot, dry summers, despite the increments in flow from the springs." Johnson (1958:16, 17) reported an average annual discharge probably of less than six cfs for Chalk Creek and three cfs for Twin Butte Creek. Bradley *et al* (1957:29) noted that during years of high precipitation there was some discharge in Twin Butte Creek but that in dry years it flowed only after heavy precipitation.

In August, 1961, I was unable to find running water or any fishes in either Twin Butte Creek or Chalk Creek. On April 1, 1962, however, I found both running water and fishes in the lower part of Chalk Creek, although Twin Butte Creek was dry. Fishes taken in Chalk Creek at that time were *Semotilus atromaculatus, Notropis stramineus missuriensis, Notropis l. lutrensis, Pimephales promelas, Campostoma anomalum pullum, Fundulus kansae, Ictalurus melas, Lepomis cyanellus, Lepomis humilis,* and *Etheostoma spectabile*

pulchellum. Specimens of *S. atromaculatus, C. a. pullum* and *E. s. pulchellum* were in breeding condition. The fish faunas of these creeks of the Chalk Bluffs Area of Gove and Logan counties is seemingly limited to species that ascend the streams from the somewhat more permanent Smoky Hill River during periods when running water is present. Few fish probably survive the summer in these streams.

The Pierre Shale that overlies the Niobrara Chalk resembles the latter in being a poor aquifer but an excellent aquiclude. The aquicludal properties of the Niobrara Chalk and the Pierre Shale are important in relation to the overlying Ogallala Formation of Pliocene age that covers a large part of the High Plains.

Ogallala Formation

In much of the Basin of the Kansas River, west of a line from Ness to Smith counties, Kansas, to Adams County, Nebraska, the Ogallala Formation is present. Its thickness varies from a featheredge in the east to at least 350 feet in western Kansas (Bayne, 1956:25). According to Frye, Leonard, and Swineford (1956:8) the formation in northern Kansas is a heterogeneous complex of clastic deposits ranging from coarse gravels to clay, uncemented or variably and variously cemented by opaline or calcareous cements. Frye and Leonard (1959:12) interpreted this heterogeneity as the result of a "random intermixture of channel and flood-plain environment of deposition." Further aspects of the environment of deposition of this formation are discussed elsewhere. Along many stream valleys, particularly along that of the upper Smoky Hill River, the Ogallala Formation has been removed by erosion and Cretaceous bedrock is exposed. Much of the formation has also been mantled by loess, dune sand and Pleistocene sands and gravels. Frye and Leonard (1959:6) stated "The Ogallala formation is of great economic importance throughout the Great Plains, primarily because it constitutes the largest and most extensive groundwater reservoir of the region." By virtue of this quality, the formation is stressed here.

The aquicludal nature of the underlying Niobrara Formation or Pierre Shale has been mentioned above. Springs occur at many localities where the contact between the water-bearing Ogallala formation and the underlying aquicludes is exposed. Bradley *et al* (1957:50-53) mentioned such springs in Rose Creek valley and along Eagle Tail Creek in Wallace County and along Ladder Creek

in Scott County State Park, where one spring, called Big Spring, is reported to yield 400 gpm. These authors further observed (p. 53) "Many springs rise in other tributaries of Smoky Hill River, particularly in Hell and Salt creeks in the eastern part of the area. The contribution from the Ogallala formation by such spring discharge to the flow of Smoky Hill River east of Ladder Creek is considerable." Walters (1956:30) described similar springs along Beaver Creek in Rawlins County: "Water moving laterally at the base of the Ogallala formation on the top of the impermeable Pierre shale flows or seeps out at the surface where the top of the Pierre shale is exposed. Beaver Creek, which is an effluent stream, has many inconspicuous seeps along its entire course and receives considerable water from the ground-water reservoir." The permanency of the water supply derived from the Ogallala Formation was indicated by Johnson (1958:48, 49) in describing ground water conditions in Logan County, Kansas. In wells measured periodically he found little or no influence on water-level by seasonal or year-to-year variations in precipitation. Long-term trends in precipitation possibly were reflected in the water levels after a lag of about three and a half years.

The springs and seeps deriving their discharge from the Ogallala formation are of paramount importance to aquatic life in this semiarid region. Areas in which springs are especially numerous are the upper Smoky Hill Valley, where aquifer and aquiclude are exposed, and along the valley of the upper Republican River and the lower courses of its tributaries where dissection has been great enough to expose Cretaceous aquicludes (Bradley and Johnson, 1958:599, 603). Much of the lower course of Medicine Creek (Frontier Co., Nebraska) is cut in Cretaceous bedrock due to the fact that this stream parallels roughly the crest of the Cambridge Arch, which raises lower strata (Bradley and Johnson, 1958:599). Medicine Creek, then, receives water from springs at the contact of Pliocene and Cretaceous rocks and in this respect differs from Red Willow Creek to the west and from the streams that receive water from Pleistocene gravels to the east. Noteworthy among the springs in the Republican drainage are those along Rock Creek in Dundy County and along the North Fork Republican River near Wray, Colorado; at both localities small fish hatcheries have been built. Table 3 indicates the species of fishes recorded for Wallace County, Kansas, and for Dundy County, Nebraska—areas in which springs issuing from the Ogallala Formation supply much water to streams. From the two areas a total of 30 species has been recorded.

For this longitude in the High Plains this is a surprisingly large number of species. Collections from the area east of the Ogallala Escarpment in the Dissected High Plains District of Kansas rarely contain more than ten species of fish. Several collections made in Rose Creek and in the Smoky Hill River (combined species list) near Wallace, Kansas, have yielded the following numbers of species: 13 (collection by Taylor, 1950); 16 (collection by Cross and Nelson, 1958); and 15 (collection by me, 1961).

Notropis blennius and *Hybognathus hankinsoni* have been taken almost exclusively in the High Plains part of the Kansas River Basin where spring-fed, permanently-flowing streams occur.

Kansas River Basin in Nebraska

Most of that part of the Kansas River Basin in Nebraska cannot be placed in the physiographic subdivisions that have been employed for Kansas, although the basin is almost entirely within the Great Plains Physiographic Province (Fenneman, 1931:4). This difficulty is mainly due to the greater degree of mantling by glacial till, loess, dunesand, and fluviatile sands and gravels that occurred in Nebraska during Pleistocene time. To my knowledge no detailed study of the physiography of Nebraska has been undertaken.

Loess Plains (*Loess Hills*)—In the Kansas River Basin the Illinoian and Wisconsinan glacial ages were times marked by the deposition of fine, in great part eolian, sediments. There are three stratigraphic units of the post-Kansan Pleistocene of which "loesses" or silts are prominent components. These are, oldest to youngest, the Loveland Silt of Illinoian age (Frye and Leonard, 1951:293-295) and the Peoria and Bignell silts of Wisconsinan age (Frye and Leonard, 1951:298-303). All have been ranked as members of the Sanborn Formation by Frye and Fent (1947:42).

Although the origin of "loess" has been a subject of controversy, there seems to be agreement that the late Pleistocene loesses of Kansas and Nebraska are almost entirely eolian in origin (Lugn, 1935:130ff., 161ff.; Swineford and Frye, 1951:317). Thicknesses of loess are great enough in most of south-central Nebraska between the Platte and Republican rivers to have physiographic importance (LH in Fig. 2).

Most of the Kansas River Basin west of the Big Blue River and north of the Republican River seems best assigned to the Loess Plains District. (A small part of the Big Blue River Basin in Seward, Lancaster, Saline, Gage, and Jefferson counties, Nebraska,

TABLE 3.—SPECIES OF FISH TAKEN IN (1) TRIBUTARIES AND MAINSTREAM OF SMOKY HILL RIVER IN WALLACE COUNTY, KANSAS, (2) TRIBUTARIES AND MAINSTREAM OF REPUBLICAN RIVER IN DUNDY COUNTY, NEBRASKA, AND (3) SOUTHWARD-FLOWING TRIBUTARIES ON THE NORTH SIDE OF THE REPUBLICAN RIVER IN FRANKLIN AND WEBSTER COUNTIES, NEBRASKA. (1) AND (2) ARE FED BY SPRINGS ISSUING FROM THE BASE OF THE OGALLALA FORMATION; (3) DRAINS AN AREA UNDERLAIN BY PLEISTOCENE SANDS AND GRAVELS.

	(1) Wallace Co., Ks.	(2) Dundy Co. Nebraska	(3) Republican tributaries
Cyprinus carpio	X	X	X
Semotilus atromaculatus	X	X	X
Hybopsis gracilis		X	X
Hybopsis biguttata	X		
Hybopsis storeriana		X	
Hybopsis aestivalis		X	
Phenacobius mirabilis	X		X
Notropis cornutus	X		
Notropis lutrensis	X	X	X
Notropis blennius	X	X	
Notropis stramineus	X	X	X
Hybognathus hankinsoni	X	X	X
Hybognathus placitus	X	X	X
Pimephales notatus	X		
Pimephales promelas	X	X	X
Campostoma anomalum	X	X	X
Carpiodes cyprinus		X	
Carpiodes carpio	X	X	X
Catostomus commersoni	X	X	X
Ictalurus punctatus	X		X
Ictalurus natalis	X		X
Ictalurus melas	X	X	X
Noturus flavus	X	X	X
Fundulus kansae	X	X	X
Micropterus salmoides		X	
Lepomis cyanellus	X	X	X
Lepomis humilis	X	X	X
Lepomis macrochirus		X	
Pomoxis nigromaculatus		X	
Etheostoma spectabile	X	X	X
Total	23	24	20

can be assigned to the Glacial Till Plains District discussed heretofore.) Fenneman (1931:21, 22) discussed the Loess Plains District only briefly, applying the term to an area east of the Sandhills District and adding, "To the south the loess overlaps the flat uplands of the typical High Plains, thinning out in northern Kansas where it merges with the general soil sheet . . ." That a loess mantle is also widespread over much of the upland surface of northwestern Kansas has been pointed out by Hibbard *et al* (1944:6). In a generalized areal mantlerock map of Nebraska, Condra and Reed (1959: Fig. 3) indicated that nearly all of the Kansas River Basin

west of the Big Blue River in Nebraska is covered by loess. Exceptions are areas in which stream erosion has removed the loess cover or where dunesand has been deposited rather than loess. These areas of dunesand in the Kansas River Basin are mainly in Dundy, Chase, Perkins, Lincoln and Hayes counties in southwestern Nebraska. They are surrounded by plains of loess, are scattered in occurrence, and seem better referred to the Loess Plains District than to the Sandhills District. To the south and west the mantle of loess gradually becomes thinner over northwestern Kansas and eastern Colorado and is, consequently, of less importance physiographically than in Nebraska, even though overlying most of the surface of the Ogallala Formation.

The surficial mantle of the Loess Plains overlies various other, often intervening, sediments in addition to the Ogallala Formation of the High Plains; in some cases these underlying sediments are of more importance to the regimen of streams in the area than is the loess cover itself.

In parts of the drainage of the Big Blue River in Saline, Jefferson, Polk, Butler and Seward counties, Nebraska, and notably in the drainages of Lincoln Creek, Beaver Creek, and North Branch Blue River, loess overlies glacial till. Neither loess nor glacial till is effective as an aquifer; thus, streams receive little discharge from this doubly thick mantle. Streams have done little valley-cutting in the area, gradients are only a few feet per mile, and bottoms are of fine, tenacious silt derived from the loess mantle. Water in these streams is characteristically highly turbid; banks are low but steep and the streams resemble miniature canyons winding across the loess mantle. These streams are some of the poorest within the basin in terms of condition of water and diversity of fauna. The only species found in September, 1961, were *Pimephales promelas* and *Ictalurus melas,* which were common, and *Lepomis cyanellus,* which was rare. The crayfish *Orconectes nais* was abundant at some stations. Even in the 1800's the fauna in this area seems to have contained few species. Evermann and Cox (1896:349), at four stations in this area, obtained only the following species: *Semotilus atromaculatus, Notropis l. lutrensis, Notropis stramineus missuriensis, Pimephales promelas, Ictalurus melas, Noturus flavus* (USNM 76123), and *Lepomis humilis.* At Seward, Nebraska, on Lincoln Creek, Evermann and Cox secured only one species—*Notropis l. lutrensis.* They noted that the water at all stations was muddy. Downcutting by streams west of an area where loess

overlies water-bearing sands and gravels of Pleistocene age (discussed below) generally has not been deep enough to remove the thick deposits of loess and of the Ogallala Formation so as to expose the Ogallala-Cretaceous contact, which is often spring-bearing. Bradley and Johnson (1958:600) reported that both the Loveland Loess and Peoria Loess in uplands of this area may reach thicknesses of 60 feet each. The overlying Bignell Loess is as thick as 40 feet in places, and the underlying Ogallala Formation as thick as 400 feet. Bradley and Johnson (1958:611) noted that recent alluvium is the common aquifer for stock and domestic wells in the smaller tributary-valleys. These wells are shallow and often go dry. Presumably such Recent alluvium also furnishes scant amounts of water to streams. The area is poorly watered. Red Willow Creek in July, 1961, after flowing for a distance of more than 50 miles, seemed to carry less water than did creeks such as Elm Creek in Webster County (draining an area of Pleistocene sands and gravels) that were less than 20 miles long.

In addition to separating the level of drainage-channels from that of the water table, the great thicknesses of loess further modify streams by contributing fine silt, which renders the water turbid and forms stream-beds of fine, tenacious silt. Streams such as Red Willow Creek and Stinking Water Creek resemble those farther east where loess overlies glacial till in the valley of the upper Big Blue River. A Secchi disc reading in Medicine Creek above the area of Cretaceous and Pliocene outcrops on August 22, 1961, was eight inches. The fauna is impoverished; fishes taken in Red Willow Creek were *Cyprinus carpio, Hybopsis gracilis, Notropis l. lutrensis, Notropis stramineus missuriensis, Lepomis cyanellus, Lepomis humilis* and *Pomoxis annularis.*

In extreme western Nebraska and in much of the Basin in eastern Colorado, as in northwestern Kansas, the mantle of loess thins and the Loess Plains gradually merge into the typical High Plains in which the surface of the Ogallala Formation is relatively lightly mantled.

Pleistocene Sands and Gravels—To the west of the glaciated area described above the loess mantle lies upon another mantle composed of fluviatile sands and gravels of Pleistocene age. Lugn (1935:88) placed these fluviatile sediments west of the glacial till area in four formations: Holdrege, Fullerton, Grand Island, and Upland, all comprising the "Platte series," which is distributed over 15,000 to 20,000 or more square miles in south-central Nebraska.

Frye and Leonard (1952:Fig. 2) ranked (1) the Holdrege and Fullerton as members making up the Blanco Formation and (2) the Grand Island and Sappa (= Upland Formation of Lugn, 1935) as members making up the Meade Formation. Of chief interest here are the Holdrege and Grand Island members, which in Nebraska are, according to Lugn (1935:92, 103), predominantly sands and gravels of quartz and other granitic and metamorphic crystalline minerals and rock fragments. Both members are coarse toward the base and become finer toward the top. The Fullerton and Sappa members, which succeed in Nebraska the Holdrege and Grand Island members, respectively, consist of clay, silts, and fine sands. Frye and Leonard (1952:Fig. 1) indicated a time of deposition for the Holdrege Formation from the time of maximum Nebraskan glaciation until late in the Nebraskan Age. They indicated a similar correspondence of the Grand Island Member and the Kansan glaciation (p. 104, Fig. 1), with deposition of the Sappa Member extending into early Yarmouthian time.

The great geographic extent of these gravels and their unique history seems first to have been properly appreciated and explained by Lugn (1935:81-127). As visualized by Lugn these gravels and sands accumulated as "inwash-outwash" sediments west of the glaciated areas in eastern Nebraska and Kansas. That is, around the glacial margins, barriers must have been formed, either contemporaneously or successively, by glacial ice, moraines, and other features of glacial till. Drainage was to the west and south away from these barriers (especially during the time of glacial melting). At the same time streams swollen by pluvial conditions and, in some cases, receiving in their upper parts meltwaters from glaciers of the Rocky Mountains brought great amounts of sediments into south-central Nebraska from the west and north. Thus both inwash and outwash contributed to accumulation of deposits of sands and gravels. During Holdrege time sands and gravels were laid down in pre-existing valleys to be overlain in turn by finer sediments during Fullerton time. As sediments (Grand Island and Sappa) continued to be added, valleys were filled, transgressed, and a coalescent sheet of clastics covered a great part of south-central Nebraska (Lugn, Fig. 5).

In some of the areas discussed above a stratum of heterogeneous clastic materials was laid down above the silts and clays of the Sappa Formation. This unit has been termed the Crete Member by Frye and Leonard (1951:293), who considered it to be Illinoian in age. The Crete sands and gravels are far less widespread than

are those of the Holdrege and Grand Island members and are relatively thin. According to Lugn (1935:129) the Crete Member attains thicknesses of at least 35 feet. It is locally significant as a source of ground water.

The thickest fluviatile deposits occur in the counties west of the glacial till border in Nebraska. Sands and gravels extend as far west as Medicine Creek, but thin considerably towards the west in the Republican River Valley. According to Lugn (1935:104) the Grand Island member "ranges in thickness from 30 to perhaps 150 feet, but averages about 75 feet." In the area directly north of the Republican River the fluviatile sheets of sands and gravels are not coalescent but break up and almost fill narrow, steep-sided valleys ("outlet valleys") that existed along the north side of the ancestral Republican River in pre-Holdrege time (Lugn, 1935:113). These outlet valleys are now occupied by short, permanently-flowing tributaries of the Republican River that obtain their water from the gravels considered here. Contemporaneous fluviatile gravels extend into adjacent northern Kansas in northern Republic County (Lugn, 1935:196) and along the valleys of Big and Little Blue rivers and Mill Creek in Marshall and Washington counties.

Due to the efficiency of the Holdrege and Grand Island gravels and sands as aquifers, streams in this area contrast greatly with those just described in the area where loess mantles glacial till. Lugn (1935:203-207) pointed out that the configuration of the level of the water table of the area discussed here is inclined downward toward the south, thus allowing subsurficial flow of water from the Platte River Valley southward. The water emerges in tributaries of the Little Blue River and the Republican River. Not all streams in the area are perennial, however. The depth to the water table is variable and dependent on the thickness of the overlying loess strata, dissection of the land, and nature and extent of the water-bearing sediments. Johnson and Keech (1959:20) noted that the water table is approximately 75 feet below the valley of the West Fork of the Big Blue River north of Hastings, Nebraska. Westward and southward from these tributaries of the Big Blue River a greater amount of perennial stream flow exists in the basin of the Litle Blue River and in south-flowing tributaries of the Republican River in Nuckolls, Webster, Franklin, and Harlan counties, Nebraska. However, the upper parts, even of these streams, are above the water table and are highly intermittent. Where the level of the stream channel intersects the level of the water table streams become effluent and, in some cases, pick up considerable volume

over a relatively short distance. Thus, on July 19, 1961, I noted that Elm Creek in Webster County changed in a distance of less than two miles from a dry stream bed to a flowing stream (with fish) carrying several cubic feet per second. On September 9, 1961, the upper portion of the Little Blue River was highly intermittent to completely dry above Holstein (Adams County, Nebraska) but accrued a considerable volume of flow in a distance of a few miles south of Roseland, Adams County.

Effluent parts of streams of this area resemble greatly, due to their permanency of flow, those streams that are fed from permanent springs issuing from the base of the Ogallala Formation. Typically the streams are shallow and braided, with clear, cool water flowing briskly over sandy bottoms. The streams have not been affected greatly by settlement or cultivation, because they are fed from springs generally in or along the stream-bed itself; runoff from upland areas occurs only in times of heavy rainfall. Cultivation is not extensive because streams have dissected the non-resistant loess mantle and formed deep, steeply-walled valleys.

The fauna of the streams resembles that found in the spring-fed streams of Wallace County, Kansas, and Dundy County, Nebraska. A comparison of species that have been taken in the three areas is presented in Table 3. The crayfish *Orconectes n. neglectus* has been taken in Cottonwood Creek, Franklin County, Nebraska, and in Elm Creek, Webster County, Nebraska. Elsewhere in the Kansas River Basin it has been found in recent years only in streams draining areas of contact between Pliocene and Cretaceous rocks in Dundy County, Nebraska, and Yuma County, Colorado, and in the Flint Hills area of Kansas. Amphipods (species undetermined) occur in springs of this area, in Dundy County, Nebraska, in Wallace County, Kansas, along the Shawnee Escarpments in the Osage Cuestas, and in the Flint Hills.

To the west the Pleistocene gravels become thinner. It has been noted previously that much of the lower course of Medicine Creek was cut down to Cretaceous and Pliocene bedrock due to the presence of the Cambridge Arch. West of Medicine Creek, Pleistocene gravels are limited mainly to the valley of the Republican River, and in the area north of the River loess deposits or sand dunes lie directly on bedrock of the Ogallala Formation.

KANSAS RIVER SYSTEM PRIOR TO SETTLEMENT

Extensive archeological work in the Basin has failed to reveal much information concerning fishes. Concerning the Pawnee In-

dians, Wedel (1936:62) noted that "Fish appear to have been used but little, as their bones are seldom present in the refuse-filled caches." The Pawnee Indians were inhabitants of the middle reaches of the Kansas River Basin, north and west of Big Blue River. Whether the more sedentary Kansa Indians that inhabited the better-watered lower part of the Basin made greater use of fish is not known, but Wedel (1946; 1961) did not list remains of fishes or artifacts connected with fishing in his discussions of their archeology. Explorers who visited the Kansa Indians in the 1800's such as Thomas Say (Thwaites, 1905c), Frederick Chouteau (Adams, 1904), and Father Pierre Jean DeSmet (Thwaites, 1906a), although discussing foods of the tribe, did not mention the use of fishes.

Reports of their use by white pioneers are equally rare, although Carey (1954:89) quoted a letter of George O. Willard from Juniata, on the Big Blue River a few miles north of present Manhattan, Riley County, Kansas: "The river is filled with fish weighing from one to one hundred pounds. I ate a portion of one caught in the Kansas, which weighed 76 pounds." Similar accounts of large fishes in the rivers of the lower part of the basin in the 1800's have been given by Snow (1875) and Dyche (1914).

The condition of streams in the Kansas River Basin prior to the time of the Louisiana Purchase is virtually unknown. Wedel (1941:24-27) inferred from archeological and sedimentational observations that droughts, some sufficient to depopulate the western plains, had occurred repeatedly in prehistoric times. Among the earliest recorded observations are those of Lewis and Clark (Thwaites, 1905b:35) as they passed the mouth of the Kansas River during their explorations of the newly-acquired Louisiana Purchase. The first explorer to leave a fairly detailed journal concerning parts of the Kansas River Basin was Zebulon Pike, who twice crossed the Smoky Hill, Saline and Solomon rivers while traveling from southern Kansas to and from a Pawnee Indian village on the Republican River. In 1819 and 1820 a party of exploration under the command of Major S. H. Long traveled across the Great Plains to the Rocky Mountains and back. Accompanying Long on this expedition was Thomas Say, noted American naturalist. Say was a member of a detachment that left the main party to explore the lower Kansas River Valley as far as its confluence with the Big Blue River Valley. Frederick Chouteau was a trader with the Kansa Indians from about 1829 to 1853. During part of this period, he plied up and down the Kansas River between a trading

outpost near Mission Creek in present Shawnee County and a settlement near the mouth of the Kansas River. His reminiscences have been recorded by Adams (1904). Maximilian, Count of Wied-Neuwied, a rhenish German interested in natural history, participated in a voyage up the Missouri River in 1833. In 1842 and 1843 Col. John C. Fremont traversed parts of the Kansas River Basin while carrying out his famed explorations of the West.

Lower Mainstream

These explorers and observers recorded a number of impressions about the lower mainstream of the Kansas River. Concerning width, Fremont (Smucker, 1856:74) found the river near present Topeka, Kansas, on June 14, 1842, to be swollen from recent rains and approximately 230 yards wide. Joel Palmer (Thwaites, 1906b:38) also found the river at Topeka swollen and "about two hundred and fifty yards in width."

Observations regarding current and depth of water indicate considerable temporal variation, then as now. Lewis (Thwaites, 1905b:35) noted that the current was "gentle," whereas Fremont found the river at the date and place noted above to be "sweeping with an angry current." Clark (Thwaites, 1905a:385) noted that his party on September 15, 1806 ". . . passed the enterance of the Kanzas river which was very low." Maximilian (Thwaites, 1905d: 251) also found the river to be "very shallow" at its mouth in April, 1833. Chouteau (Adams, 1904:428) indicated extreme fluctuation in depth of the Kansas River in the 1830's: "Going down it sometimes took a good many days, as it did going up, on account of low water. I have taken a month to go down from my trading-house at American Chief (or Mission) creek, many times lightening the boat with skiffs; other times going down in a day." The crafts in which Chouteau made these journeys were pirogues—boats sixty or seventy feet long and about four feet wide, two of which were lashed together; they were capable of carrying 10 to 15 tons (Adams, 1904:428). Thomas Say's impression (Thwaites, 1905c:185) of the Kansas River near present-day Topeka in August, 1819, was of a river "so shoal as at almost any point to admit of being forded without difficulty." Several explorers, however, found the river too swollen with floodwaters to be forded when observed by them. Mention has been made above that Fremont found the river high at Topeka in June, 1842. As far upstream as the confluence of the

Republican and Kansas rivers, Fremont on June 8, 1843, found it impossible to ford the river (Smucker, 1856:193). In July, 1844, while camped along the Smoky Hill River (Smucker, 1856:490) a heavy rainstorm caused rapid flooding of the Fremont campsite, ruining many of the perishable collections of the party.

Turbidity seems also to have been variable in the lower mainstream before settlement of the watershed. Lewis wrote (Thwaites, 1905b:35), probably from second-hand information since the party did not ascend the Kansas River, that in summer and autumn the waters of the Kansas River were transparent. Long (Thwaites, 1905c:173) noted that the Kansas was less turbid than the Missouri except at times of high floods. Maximilian (Thwaites, 1905d:251) described effluent from Kansas River: "Its clear green water was distinguished by a well-defined, undulating line, from the muddy stream of the Missouri." However, Fremont observed (Smucker, 1856:74) on June 14, 1842, that the river was "yellow and turbid as the Missouri."

Lewis (Thwaites, 1905b:35) wrote that the bed of the river was "composed of soft loam, gravel and sand." More detailed descriptions of the bottom were recorded in the survey of Lt. Joseph L. Tidball, summarized below.

Concerning banks and streamside flora of the lower mainstream, Thomas Say (Thwaites, 1905c:185) noted that "Willow islands, moving sand-bars, and *falling-in* banks, are as frequent as in the Missouri. The line of forest which skirts the banks, including the bed of the river, is about half a mile wide, but not entirely uninterrupted. The course of the river is remarkably serpentine, forming woodland points alternately on both sides." Major Long wrote (Thwaites, 1905c:173,174), "Its valley, like that of the Missouri, has a deep and fertile soil, bearing similar forests of cottonwood, sycamore, &c., interspersed with meadows; but, in ascending, trees become more and more scattered, and at length disappear almost entirely, the country, at its sources, being one immense prairie." Fitch and McGregor (1956) in an examination of early records concerning forested habitat in the area of Lawrence, wrote (p. 126) "In the Kansas River flood plain and small tributary valleys, rich mesophytic forest of predominantly oak-hickory type was present."

Most informative of the early accounts concerning the lower mainstream is that of Lt. Joseph L. Tidball, who, in August, 1853, made a survey of the Kansas River from Ft. Riley, Geary County, to its mouth, in order to determine the navigability of the river.

He found the water too turbid to ascertain depth visually and made recourse continually to a sounding rod. He stated (Langsdorf, 1950:149):

"This process, though vexatious and wearisome, was attended with the advantage of giving a more accurate knowledge of the general depth of the water than could have resulted from less frequent soundings. This system of soundings showed the general depth of water in the main channel, for a distance of fifty miles, or thereabout, [downstream from Ft. Riley] to be from two to seven feet; that is, it varied between these limits, more frequently exceeding the greater than falling below the less . . ."

Tidball noted all areas in which the depth averaged less than two feet and found nine such areas between Ft. Riley and the mouth of the Blue River. Along this part of the river he found the average width to be approximately 80 yards, occasionally widening to 120 or more yards. Between the mouth of the Blue River, which was observed to be 60-80 yards wide and 2.5-4 feet deep, and the mouth of Soldier Creek the river widened. Between Soldier Creek and the mouth of the Kansas River the stream again became narrower. Tidball frequently mentions the presence of large sandbars; for instance, approximately 12 miles above the mouth of the Vermillion River he observed (Langsdorf, 1950:151):

". . . series of little bars, disposed like ribs across the channel, with not more than eight inches of water on some of them, while below and between them it was not unfrequently six or seven feet deep."

Tidball mentions another area below the present location of St. Marys in which shoals as shallow as 12 inches prevailed for approximately one mile. Regarding the bottom, Tidball wrote, (Langsdorf, 1950:154):

"Except in a few places to which allusion has been made, at the rapids and in their vicinity, the bed of the river is an easily yielding quicksand, and its surface broken."

In regard to the banks, he noted (Langsdorf, 1950:155):

"The banks of the upper portion of the river are formed almost entirely of sand, occasionally mingled with clay. Lower down, this is seen in somewhat greater abundance, sometimes in thin strata alternating with sand; occasional beds of gravel and in a few places, for short distances, rocky developments occur."

Tidball surmised that he descended the river at a time of "low water." He found evidence and received testimony from streamside residents that the river-level had been 5 to 8 feet higher earlier in the same year. He formed the opinion that high water in spring and early summer was sufficiently characteristic of the stream to allow navigation during that part of the year.

Tributaries

References to tributaries of the Kansas River before settlement are few.

Thomas Say (Thwaites, 1905c:186) crossed the Vermillion River in present Pottawatomie County, Kansas, remarking that it was four feet deep and approximately twenty yards wide. Concerning Blue River a mile or two above its mouth, Say (Thwaites, 1905c: 200) reported a width of 25 yards and a maximum depth of three feet. Fremont (June 20, 1842) found the lower Blue River to be (Smucker, 1856:79), ". . . a clear and handsome stream, about one hundred and twenty feet wide, running with a rapid current . . ." Proceeding northwestward in the Blue River Basin, Fremont described some creeks as "handsome" with clear water and sandy beds, and mentioned others that were dry. After encountering several of the latter, Fremont wrote (Smucker, 1856:80), ". . . after a hard day's march of twenty-eight miles, encamped, at 5 o'clock, on the Little Blue, where our arrival made a scene of the Arabian Desert. As fast as they arrived, men and horses rushed into the stream, where they bathed and drank together in common enjoyment." Fremont found Little Blue River at this place to be approximately 50 feet wide and three to four feet deep.

Zebulon Pike traversed central Kansas in September and October, 1806, and noted (Hart and Hulbert, 1932:73-76) various tributaries that were dry. Pike judged (p. 73) Smoky Hill River near present-day Bridgeport, Saline County, Kansas, to be 25 or 30 yards wide, and navigable in flood seasons. Returning east from his Expedition of 1843-44 in July, 1844, Fremont descended Smoky Hill River, describing the journey as follows (Smucker, 1856:489):

> "On the evening of the 8th we encamped in a cottonwood grove on the banks of a sandy stream-bed, where there was water in holes sufficient for the camp. Here several hollows, or dry creeks with sandy beds, met together, forming the head of a stream which afterwards proved to be the Smoky Hill fork of the Kansas River.
>
> "As we traveled down the valley, water gathered rapidly in the sandy bed from many little tributaries; and at evening it had become a handsome stream, fifty to eighty feet in width, with a lively current in small channels, the water being principally dispersed among quicksands.
>
> "Gradually enlarging, in a few days' march it became a river eighty yards in breadth, wooded with occasional groves of cottonwood."

Previously enroute westward, Fremont found (Smucker, 1856: 196) Prairie Dog Creek to be ". . . forty feet wide and four feet deep" on June 23, 1843. On June 26, 1843, approximately 80

miles farther west, Fremont came to the South Fork of Republican River (Smucker, 1856:196): ". . . whose shallow waters, with a depth of only a few inches, were spread out over a bed of yellowish white sand 600 yards wide."

Regarding the appearance of valleys of tributaries, Say remarked (Thawites, 1905c:200) that along the Big Blue River near present-day Manhattan, Kansas, "The soil supports but a thin growth of grass, and the timber is far from abundant, consisting principally of different sorts of oak, confined to the margin of the creek, its ravines and tributaries." Of the Little Blue River Fremont wrote (Smucker, 1856:81), "Our route the next morning lay up the valley, which, bordered by hills with graceful slopes, looked uncommonly green and beautiful. The stream . . . fringed by cotton-wood and willow, with frequent groves of oak, tenanted by flocks of turkeys." Fremont found Prairie Dog Creek (Smucker, 1956:196) to have "a dense border of wood, consisting principally of varieties of ash" but approximately 100 miles farther west on the Republican River (pp. 196, 197): "With the exception of one or two distant and detached groves, no timber of any kind was to be seen; and the features of the country assumed a desert character, with which the broad river, struggling for existence among the quicksands along the treeless banks, was strikingly in keeping." None of these reports of conditions in the tributaries prior to settlement mention silty bottoms although several mention sand or "quicksand."

In October and November, 1869, exploration pursuant to planning a railroad route was undertaken in the Solomon River Valley by a party under the leadership of Mr. Robert McBratney. Entries from McBratney's diary have been published by Caldwell (1937). In reading these comments it should be borne in mind that McBratney was interested in promoting settlement of the Solomon Valley. On October 21, 1869, McBratney noted (Caldwell, 1937:64, 65):

"Crossed the S. B. of S. [South Fork of the Solomon] and struck out for the Waconda or great spirit spring of the Indians, which is about four miles below the forks. Three miles below camp crossed the main Sol. and have thus crossed all branches. Find about the same amt. of water in all, that is a stream about 50 ft. wide and from two to three feet deep, at this its dryest. Water clear and pure, & excellent for drinking."

On this same date McBratney explored several tributaries of the Solomon near Waconda Springs (Mitchell County), making the following notations (Caldwell, 1937:65, 66):

CARR CREEK—"Water in creek stopped by Beaver dams. Cr. well timbered with hard timber, and growing better up. Width of bottom ¼ to ½ mile, water good."

UNNAMED CREEK—"Examined Cr. for six to seven mile. Running water."

OAK CREEK—". . . examined Oak Cr. for seven to 9 miles. Find it nearly as large as a Br. of Solomon, with bottom 1½ miles. Well wooded with hard wood. . . . Water of Cr. running, but not strong."

Farther upstream on the North Fork of the Solomon in the vicinity of the present town of Kirwin, McBratney noted (Caldwell, 1937:69) "The water of the Solomon and its tributary is clear, pure and hard. . . ." Returning from the expedition, the South Fork of the Solomon in present Osborne County was found to be (Caldwell, 1937:73) a ". . . very much larger stream than the N. B. North Fork of the Solomon & running three times as much water."

Settlement of the western part of the Kansas River Basin lagged greatly behind that of the eastern part. This was due partly to hostility of Indian tribes of the area, chiefly the Cheyennes. Holding an important place in the history of the area was Fort Wallace, which was an active establishment until 1882 (Montgomery, 1928: 278). In 1870 the acting assistant surgeon at the post, M. M. Shearer, wrote, as reported by Montgomery (1928:242), "At this point the Smoky Hill is a comparatively beautiful stream of running water, due to one of its tributaries, which joins it about three miles west of the fort; beyond that point the river consists of occasional ponds with intervening sand beds, through which the water takes a subterranean course." Prof. Edward Drinker Cope sojourned at Fort Wallace while collecting in the Cretaceous beds of western Kansas. In September, 1871, he wrote (Osborn, 1931:163), "We found a high bluff near the Twin Buttes which we determined to search. We found Butte Creek totally dry and had to go four miles further and camp by a spring in a narrow ravine." The stream mentioned by Shearer may have been Rose Creek, which is still a permanent stream unlike the Smoky Hill River. The "Butte Creek" or Twin Butte Creek mentioned by Cope was observed by me to be dry at several places in September, 1961, and April, 1962.

Summary

The accounts cited above and others suggest that the Kansas River and its larger tributaries have long been subject to fluctuation in amount of discharge. There seems also to have been considerable fluctuation in the past, as now, in the degree of turbidity, especially

in the larger streams. That the Kansas River was not, in the middle 1800's, consistently a deep, clear stream is well-documented by Tidball's navigability survey (Langsdorf, 1950) and by numerous instances reported by Greene (1906) of steamboats going aground on sandbars during the period 1854-1866. Even for small boats such as the pirogues used by Chouteau (Adams, 1904: 428) or the grain boat employed by James R. Mead (Mead, 1906:9) water was often too shallow for navigation on the lower Kansas River.

That all upland tributaries were not permanently flowing streams is attested by early observers such as Pike (Hart and Hulbert, 1932:73, 76), Fremont (Smucker, 1856:489), Shearer (Montgomery, 1928:242), Cope (Osborn, 1931:163) and Mead (1906:15). There is some evidence, however, that streams in areas now extensively tilled were more nearly permanent and were clearer than at present. McBratney's (Caldwell, 1937) enthusiastic accounts of the clear, permanent tributaries of the Solomon suggest this, as do other descriptions quoted.

KANSAS RIVER SYSTEM AND ITS FAUNA SUBSEQUENT TO SETTLEMENT

A simplified categorization of man's effects on the rivers of the Kansas River Basin might include that which is (1) taken from and (2) added to the streams.

The first category is probably the less deleterious in regard to fishes of the Basin. Water is taken directly from the rivers and indirectly from groundwater supplies along the river for domestic and industrial use and for irrigation.

Substances added directly or indirectly to streams as a result of man's activities include (1) domestic and industrial wastes, and (2) silts and other sediments that enter in increased amounts because of modification of the land. The Kansas State Board of Health, in cooperation with municipal and industrial organizations, has carried on an effective program that has ameliorated or removed the worst aspects of the domestic and industrial pollution problem. Colby *et al* (1956:64) noted that "Throughout most of the Basin . . . municipal and industrial pollution has been to a large extent controlled. Only in the Kansas City area do serious problems still exist" where ". . . the last four miles of the Kaw's course . . . approximates an open sewer." In the central part of the Basin, oil-field brine was formerly led into streams. As some rivers in the same area (for example the Saline and Smoky

Hill rivers) were naturally highly saline, a condition inimical both to man and to some aquatic organisms was created. At present, however, most brine is reinjected into deep-lying rock strata. Although parts of the Kansas River System may long have been at least periodically turbid, intensive cultivation of the land in many parts of the Basin seems to have increased turbidity and siltation of streams.

The highly variable nature of precipitation patterns in the Kansas River Basin with recurrent droughts is interrelated with the conditions discussed above. In hot, dry years more water is needed by the public at the same time that streamflow is minimal; increasing population in the Basin intensifies this problem. In the drought year, 1954, according to Colby *et al* (1956:61), sixty-one municipal water supply systems in that part of the Basin in Kansas were inadequate in providing necessary amounts of water. Furthermore, reduced flow may decrease the ability of streams to transport wastes and sediments and to recover from pollutants.

In July, 1885, O. P. Hay traveled in northwestern Kansas, collecting fishes at several localities. His published account (1887) contains several references to stream conditions at that time. Of a small tributary of the Solomon River immediately west of Beloit, Mitchell County, Kansas, Hay wrote (1887:242, 243) "This stream, like all others in this part of the State, flows in a deep ravine, is very sluggish, and so filled with ooze as to make the dragging of a seine a very difficult and disagreeable task." Along the North Fork Solomon River at Kirwin, Phillips County, Kansas, Hay (1887:247) noted, "The collection obtained at this point was made in a muddy, oozy, stream. . . . Only nine species were secured as the fruits of a day's hard work." This is the same Solomon Valley described by McBratney (Caldwell, 1937—discussed heretofore), who had explored it only 16 years before the collections were made by Hay. At the time of McBratney's exploration there were virtually no white settlements in the valley and McBratney's party was accompanied by troops to fend off possible attack by Indians. It would seem that in this short period of time some siltation of stream bottoms had begun, if one interprets Hay's "muddy ooze" as evidence of erosion due to agriculture.

Farther west, however, Hay did not mention siltation, describing the North Fork Solomon River at Lenora, Norton County, Kansas (1887:248) as ". . . small, and in most places a shallow, stream, flowing with sufficient rapidity to carry away the finer materials and

leave for itself a clean bed of sand." Likewise the Saline River, 5 miles north of WaKeeney, Trego County, Kansas, was found (1887: 250) to be a ". . . shallow, rather rapid prairie brook, with a clean, sandy bed. Its depth, when visited varied from a few inches to 3 or 4 feet." Hay found the Smoky Hill River near Wallace, Wallace County, Kansas (1887:251), to be ". . . much like the Saline at WaKeeney, but smaller and more rapid."

Hay's observations suggest that siltation was notable only in eastern parts of the streams of northwestern Kansas. Today siltation seems to have progressed farther upstream. Hay's description of the North Fork Solomon River at Kirwin and the fauna he obtained there approximate the situation found today at Lenora, 50 miles to the west.

My observations along North Fork Solomon River in June, 1963, are recorded below (west to east, mileage approximate and linear, not adjusted for irregularities in the course of the river):

Mile one. Ten miles north of Hoxie, Sheridan Co., Kansas. Stream completely dry. Probably the stream west of this place was dry to its source, a distance, linearly, of approximately 50 miles.

Mile ten. Three miles SW Allison, Sheridan Co. Upland brook, up to 15 feet wide with clear water (Secchi disc reading, approximately 3 feet). Bottom of clean sand. Fringe forest of elm, ash, cottonwood and willow. Water temperature 71° F. at 11:30 a. m. Beaver dams ponding stream. Water here is obtained from springs along the contact zone of Pliocene and Cretaceous rocks.

Mile 30. Lenora, Norton Co. Creek up to 25 feet wide. Water turbid (Secchi disc reading 5 inches). Bottom of sand and silt. Fringe forest present. Water temperature 81° F. at 2:30 p. m.

Mile 55. Three miles east of Logan, Phillips Co. River up to 100 feet wide, shallow, braided. Bottom of sand and tenacious silt. Water very turbid (Secchi disc reading 3 inches). Water temperature 87° F. at 4:00 p. m.

In addition to and probably in conjunction with the changes observed in the character of the North Fork Solomon River, there seem to have been changes in the nature of the fish fauna. As indicated in Table 4, Hay took 16 species at Lenora in 1885, whereas the two collections of recent years tallied only seven and eight species. *Etheostoma spectabile*, taken by Hay at Lenora, seemingly no longer occurs there, but a population still exists 20 miles upstream in the clearer, colder headwaters at "Mile 10" mentioned above.

In Table 5 the faunal list of Hay's collection from Wallace, Wallace County, is compared with lists made at that locality in the past 25 years.

Species taken by Hay, but not subsequently at any of his stations, are *Lepisosteus osseus*, *Hybopsis biguttata*, *Chrosomus erythrogaster*, *Notropis topeka*, *Moxostoma macrolepidotum* and *Etheo-*

TABLE 4.—SPECIES OF FISHES TAKEN AT LENORA, NORTON COUNTY, KANSAS, ON THREE OCCASIONS (USNM NUMBERS GIVEN WHERE AVAILABLE).

	Hay 1885	F. B. Cross 1958	Metcalf 1963
Semotilus atromaculatus	(USNM 38233)	X	X
Chrosomus erythrogaster	(USNM 38241)		
Phenacobius mirabilis	(USNM 37962)	X	
Notropis umbratilis	(USNM 38232)		
Notropis cornutus	X		
Notropis lutrensis	X	X	X
Notropis stramineus	(USNM 37950)	X	X
Hybognathus placitus		X	X
Pimephales promelas	(USNM 38240)	X	X
Pimephales notatus	(USNM 37939)		
Campostoma anomalum	(USNM 38236)	X	X
Catostomus commersoni	X		
Ictalurus melas		X	X
Noturus flavus	(USNM 37963)		
Fundulus kansae	X		
Lepomis cyanellus	X		
Etheostoma nigrum	X		
Etheostoma spectabile	(USNM 37951)		
Total	16	8	7

stoma n. nigrum (and, indirectly, *Notropis heterolepis* if, as interpreted by Hubbs, 1951a, it was one of the parental species of the hybrid, "*Notropis germanus*" Hay). Species taken by others in subsequent years but not by Hay include only *Ictalurus natalis* and *Cyprinus carpio*. Hay's "*Ictiobus velifer*" was probably *Carpiodes c. carpio*. The only carpsucker taken by Hay that I have been able to locate (USNM 37936 from Beloit) is *Carpiodes c. carpio*.

Considering the records of Hay and other early records in light of present distribution of fishes, at least the following species seem to have suffered depletion in numbers, restriction of range, or extirpation in the Kansas River Basin in historic time: (°—doubt exists as to native occurrence in the Basin).

Ichthyomyzon castaneus
Hiodon alosoides
Hybopsis biguttata
Chrosomus erythrogaster
Notropis cornutus
Notropis h. hudsonius °
Notropis heterolepis °
Cycleptus elongatus
Carpiodes velifer
Percopsis omiscomaycus °
Stizostedion v. vitreum °
Percina maculata
Etheostoma blennioides °
Etheostoma n. nigrum
Notropis topeka

Further evidence of changes that have occurred in the aquatic fauna of the Kansas River Basin since settlement is provided by certain gastropods. Aughey (1877) listed three species of pleu-

Table 5.—Fishes Taken at Two Localities in Wallace County, Kansas. All Collections Contain Fish From the Smoky Hill River Near Wallace. In Addition, the Collections of Cross, Taylor and Metcalf Contain Fishes From Nearby Rose Creek. USNM Numbers Are Given Where Available.

Species	Hay 1885	Taylor July, 1950	Cross June, 1958	Metcalf August, 1961
Cyprinus carpio		X	X	X
Semotilus atromaculatus	X	X	X	X
Hybopsis biguttata	X			
Phenacobius mirabilis	X	X	X	X
Notropis cornutus	X	X	X	
Notropis lutrensis	(USNM 37947)	X	X	X
Notropis stramineus	X	X	X	X
Notropis topeka	(USNM 37934)			
"*Notropis germanus* Hay"	(USNM 37949)			
Hybognathus hankinsoni	(USNM 38237)	X		
Hybognathus placitus	X		X	
Pimephales promelas	X	X	X	X
Campostoma anomalum	X	X	X	X
Catostomus commersoni	(USNM 37935)	X	X	X
Ictalurus natalis				X
Ictalurus melas	X		X	X
Noturus flavus	X	X		X
Fundulus kansae	(USNM 37957)	X	X	X
Micropterus salmoides			X	
Lepomis cyanellus	(USNM 37953)		X	X
Lepomis: cyanellus x macrochirus			X	
Lepomis humilis	(USNM 37937)		X	X
Etheostoma spectabile	(USNM 37944)	X		X
Total	19	13	16	15

rocerid snails from the Blue River in Nebraska. According to Goodrich (1939:4) one of these snails was probably *Pleurocera acuta* Rafinesque; the other two seemingly were misidentifications. Probably, then, at least one species of pleurocerid gastropod formerly inhabited the Blue River System, although, to my knowledge, no pleurocerids have been reported anywhere in the Kansas River Basin in this century. *Pleurocera acuta*, seems to be intolerant of the siltation of streams that has accompanied cultivation of the land (Leonard, 1959:41). I have noted during the past seven years the extirpation of what may be one of the last colonies of this snail in the Kansas part of the Marais des Cygnes River directly south of the Kansas River. This colony seemed to be flourishing in 1956 in an area of gravelly riffles three miles east of Ottawa, Kansas. In 1958 and subsequent years, however, I was unable to find any living specimens, although dead shells remained. During

this period channel-straightening, dike construction, clearing of trees from banks, and other modifications took place due to a program of flood control upstream and to construction of a divided highway across the area.

In addition Aughey (1877:701) reported viviparid snails from the Blue River. It seems probable that these were of the genus *Campeloma*. Call (1885:52; 1886:184; 1887:17) and Hanna (1909: 96) also ascribed *Campeloma* to the Blue, Delaware, Wakarusa and Kansas rivers and to Soldier Creek. However, Branson (1963:73) suggested that a few streams in extreme southeastern Kansas ". . . may be the last ecological situations available for such clear-water species in the state." Aughey (1877:702) and Call (1885:52) reported the genus *Amnicola* from a number of localities in the Kansas River Basin. At the present time this genus seems rare in Kansas (Leonard, 1959:Fig. 20).

The present disjunct distribution and the existence of older records from intervening areas suggest that the crayfish *Orconectes neglectus* Faxon was once more widespread in the central and western part of the Kansas River Basin than at present (Williams, 1954:573; Metcalf and Distler, 1961:355).

It seems probable that the presence or absence of beavers, especially in tributaries of the western part of the Basin, may bear some relation to the kinds and numbers of fishes present. Following is a statement by James R. Mead (1906:15), one of the first settlers in the Saline River Valley and namer of many of the tributaries of the Saline River, concerning conditions in 1859:

"We crossed the Saline below some salt springs from which the river derives its saline properties, and traveled north. We soon found a large, dry, sandy creek coming from the hills in the distance; following this up we came to beaver dams and water. The beaver held back all the water in the dry season. Further along were plenty of buffalo, and where the stream came out of the buffs were groves of beautiful oak timber. The canyons were full of large cedars and no sign of an ax or of white man's presence in any of it. I had found a stream unknown.

As we drove into this beautiful spot I exclaimed, 'Boys, we have got into paradise at last!'—and that name it bears to this day, and the town of Paradise is near the spot of our first camp."

The town of Paradise is in northwestern Russell County, and Paradise Creek, which flows nearby, again supports colonies of beaver according to Henderson (1960:79). Beaver were exceedingly rare in Kansas (Henderson, 1960) at least from 1900 to 1920 and probably for an even longer time. By 1930 populations were slowly increasing, especially in the northwestern part of the state.

Henderson (1960:14) suggested that a higher population per suitable stream mile may exist in the western than in the eastern part of the Kansas River Basin due to the greater availability of cottonwood and willow, preferred food of the beaver, along these western streams. In 1961, 1962, and 1963, I observed many beaver dams along the tributaries of the Kansas River in northwestern Kansas (as at "Mile ten" on North Fork Solomon River, mentioned above). These dams seem to contribute to ponding and conservation of water in these small, shallow streams of low gradient, which otherwise possess few deep pools. Henderson (1960:27, 28) pointed out that beaver impoundments provide excellent habitat for fishes on these small western streams. Probably repopulation by beavers on these streams has enhanced piscine life in general and been especially beneficial for those species that are less tolerant of adverse conditions. Hall (1946:484) pointed out the beneficial effects of ponding by beavers on aquatic and streamside life in Nevada, and Hanson and Campbell (1963:148) found in north-central Missouri that "Beaver activity appeared to improve the carrying capacity of the stream for warm-water fishes and to provide conditions suitable for a large variety of fishes. Thus their activity helped offset the deleterious effects of floods and of man's activities, especially in the headwaters." Possibly the more widespread occurrence of fishes such as *Etheostoma spectabile pulchellum* and *Noturus flavus* in streams of northwestern Kansas in collections made between 1961 and 1963 than in those made by John Breukelman in 1938 (Breukelman, 1940a) reflects improved stream conditions partly brought about by increased ponding by beavers.

A recent and more striking kind of ponding has resulted from man's construction of large reservoirs, especially in the western part of the Basin. The principal impoundments completed or under construction are as follows:

1.	Bonny	Yuma County, Colorado	South Fork Republican River
2.	Enders	Chase County, Nebraska	Frenchman Creek
3.	Trenton	Hitchcock County, Nebraska	Republican River
4.	Harry Strunk	Frontier County, Nebraska	Medicine Creek
5.	Norton	Norton County, Kansas	Prairie Dog Creek
6.	Harlan County	Harlan County, Nebraska	Republican River

7.	Cedar Bluff	Trego County, Kansas	Smoky Hill River
8.	Webster	Rooks County, Kansas	South Fork Solomon River
9.	Kirwin	Phillips County, Kansas	North Fork Solomon River
10.	Wilson	Russell County, Kansas	Saline River
11.	Glen Elder	Mitchell County, Kansas	Solomon River
12.	Lovewell	Jewell County, Kansas	White Rock Creek
13.	Kanopolis	Ellsworth County, Kansas	Smoky Hill River
14.	Milford	Geary County, Kansas	Republican River
15.	Tuttle Creek ...	Riley County, Kansas	Big Blue River
16.	Perry	Jefferson County, Kansas	Delaware River

As concerns fishes in the Basin, the stabilization of flow and filtering effect with consequent clarification of water afforded by ponding of streams are surely of importance, although the effect on distribution of fishes below and above reservoirs of the Basin has not been elucidated. A more easily observed effect has been the introduction of both native and non-native fishes into impoundments and streams of the Basin.

Graham (1885a:78) listed 13 species that had been "planted in the waters of Kansas." Of these, six (*Salmo gairdneri, Esox lucius, Cyprinus carpio, Pomoxis annularis, Stizostedion v. vitreum* and *Perca flavescens*) occur in streams and impoundments in the Basin at present. Additional species, deemed non-native, that have been placed in waters of the Basin by man are *Salmo trutta, Carassius auratus, Ictalurus nebulosus, Micropterus dolomieui* and *Micropterus punctulatus.* Evidence is equivocal as regards native occurrence of *Fundulus sciadicus, Chaenobryttus gulosus, Ambloplites rupestris* and *Pomoxis nigromaculatus.* Following is a list, kindly supplied by Mr. Roy Schoonover, Chief, Fisheries Division, Kansas Forestry, Fish and Game Commission, of species that have been stocked in reservoirs of the Kansas River Basin in Kansas by the Forestry, Fish and Game Commission: *Esox lucius, Ictalurus punctatus, Ictalurus melas, Roccus chrysops, Micropterus dolomieui, Micropterus salmoides, Micropterus punctulatus, Lepomis macrochirus, Pomoxis nigromaculatus, Pomoxis annularis, Stizostedion v. vitreum, Perca flavescens* and *Aplodinotus grunniens.*

HISTORY OF THE HIGH PLAINS AND OF THE ANCIENT PLAINS DRAINAGE

Knowledge of the Miocene history of the Great Plains is not great. Chaney and Elias (1936:26) noted that "The floras as known, and the associated mammalian remains, point toward climatic conditions which favored the development of broad grasslands, with forests restricted to the stream borders."

In the basin of the Kansas River there are widespread deposits of Pliocene and Pleistocene age that allow insight into some aspects of the history of the Basin. Knowledge of the Pliocene and Pleistocene history of the region is, in great part, due to the efforts of Maxim K. Elias, John C. Frye, A. Byron Leonard, Ada Swineford, Claude Hibbard and their associates. Lugn (1935) presented an important summary of the Pleistocene History of Nebraska and Condra and Reed (1950) wrote concerning the correlation of the Pleistocene deposits of Nebraska.

As underlying Miocene or earlier Tertiary sediments are absent throughout most of the central and southern Great Plains, and Pliocene deposits are widespread, it seems probable that a regimen marked by erosion may have been gradually replaced by one of deposition at the beginning of Pliocene time.

The lowermost or Valentine Member of the Ogallala Formation of Pliocene age occupies the lower portions of west-east trending valleys cut in Cretaceous bedrock by previous erosional activity (Merriam and Frye, 1954:57). Frye, Leonard and Swineford (1956: 56, 61) noted that during the succeeding Ash Hollow and Kimball time, alluvium continued to be laid down in the pre-existing valleys until it began to overlap the sides of the valleys and to coalesce. These authors believed that the upper part of the Ash Hollow Formation (p. 56) "transgressed most, if not all, former divides and formed a virtually continuous coalescent sheet of alluvial material throughout northwestern Kansas and southwestern Nebraska." In regard to the Kimball Formation these authors stated (p. 61) "The Kimball was the culmination of Ogallala alluviation, and overlapped most if not all of the former bedrock divides. Its surface extended as a vast coalescent plain of regional alluviation. During Kimball deposition the former bedrock valleys were no longer effective in controlling the position or direction of flow of major streams, which became free to shift in response to load, volume, and gradient." From the above descriptions one visualizes late Pliocene streams as shallow, sediment-laden, at least periodically, and meandering over a terrain with little gradient.

After filling and transgressing the shallow valleys and coalescing, the sediments of the Ogallala Formation are thought to have come to an "erosional-depositional equilibrium" (Swineford, Leonard and Frye, 1958:114). These authors suggested that the period of surface stability was "long," with a climatic trend towards desiccation that resulted in formation of a thick caliche zone and ultimately in the pisolitic or "algal" limestone that occurs at the top of the Ogallala Formation.

Frye, Leonard and Swineford (1956:57) and Bayne and Fent (1963:363) found no evidence that the east-flowing streams of Ogallala time crossed the Flint Hills in Kansas and suggested rather that drainage was to the south, through a major valley west of the Flint Hills into the area occupied by the present Arkansas River. Supporting this view, Frye (1955:80) pointed out that high terrace deposits, predominantly of chert derived from the Flint Hills and probably of Pliocene age, are found east of the Flint Hills in Kansas, although no sediments of the kinds found in the Ogallala Formation are found east of the Flint Hills.

The Flint Hills may have acted as a watershed barrier to streams from the west due to the dip of their resistant beds to the west. In the Flint Hills of southern Kansas today, streams with high gradient are eroding from the east against the regional dip of the rocks. One, the Cottonwood River, has breached the band of hills. Streams approaching the hills from the west, however, have low gradients and do not erode up-dip eastward into the Flint Hills, but typically turn southward, paralleling the line of hills until they circumvent them or are captured by a stream, such as the Cottonwood, that has breached the hills from the east.

At the end of Pliocene time, then, a master stream (Preglacial Plains Stream) is thought to have flowed north to south across the present state of Kansas west of the Flint Hills (Fig. 3). This stream seems to have been fed almost entirely by tributaries from the west. The extent of this stream system, and directions taken north and south of Kansas, are not clearly ascertainable. To the north, Lugn (1935:35-37) noted the presence in southern Nebraska, west of the Flint Hills, of three wide, buried, preglacial valleys or "Basins" that trended northwest to southeast. In central Nebraska the preglacial topography was higher, suggesting that these streams had their headwaters in the general area presently occupied by the Loup rivers. Lugn (p. 153) wrote ". . . the waters of the early Pleistocene, and before that even, the pre-Pleistocene North Platte River found escape southeastward across the inwash-outwash plain of the south

central part of the state, that is through the Holdrege or even the Hastings basin." Lueninghoener (1947:60) suggested that the Loup rivers might be former upper tributaries of a system of which the Blue River is now a lower remnant. Sharp turns to the northeast where each tributary of Loup River joins the mainstream suggest capture from a former southeasterly course such as might have existed preglacially. In summary, probably the upper Platte and the Loup rivers, but possibly not the upper Niobrara, were once part of the Preglacial Plains Stream (Fig. 3). Horberg and Anderson (1956:Figs. 1 and 2) held a different view and tentatively indicated outflow of both Preglacial Platte and Niobrara eastward into the Ancestral Mississippi.

To the south, widespread fluvial deposits along the southern boundary of Kansas (Harper to Sumner counties) indicate that the main outwash-carrying channels of the Ancestral Plains Stream of the early Pleistocene (and probably the Preglacial Plains Stream) entered Oklahoma in this area; its direction thereafter is unknown. Quinn (1958:42) theorized that the Arkansas River first breached an Ozark-Ouachita upland and emptied eastward into the Mississippi at some time in the Pleistocene prior to Sangamonian time. Probably, then, the Preglacial Plains Stream continued at least as far south as the Ancestral Red River. Faunal evidence (discussed below) suggests that drainage at some time had connections with the Ancient Red, Brazos and Colorado rivers of Texas. The presence of quartzite cobbles in high-level terraces near Dallas, Texas, older than Kansan in age (reported by Slaughter *et al*, 1963:9), suggested that drainage in that area once came from the north, crossing the area presently occupied by the valley of the Red River. The nearest outcrops of igneous rocks are in the Wichita Mountains in Oklahoma to the north. However, Frye and Leonard (1963:10-11) in describing the Hardeman Alluvial Terrace of Kansan age along the Red River east of the High Plains inferred that, by Kansan time, the Red River occupied essentially its present valley. Subsequently, Dalquest (1964:351; 1965:74) showed, on the basis of carbon 14 dates, that sediments at the type locality and at several other exposures of the "Hardeman Alluvial Terrace" were all less than 30,000 years in age, hence no older than Wisconsinan.

Southwestward there is some zoological evidence (Koster, 1957:1) that a part of the plains drainage was captured by growth headward and northward of the Pecos River and subsequent capture of eastward-flowing streams of the Ancestral Canadian System.

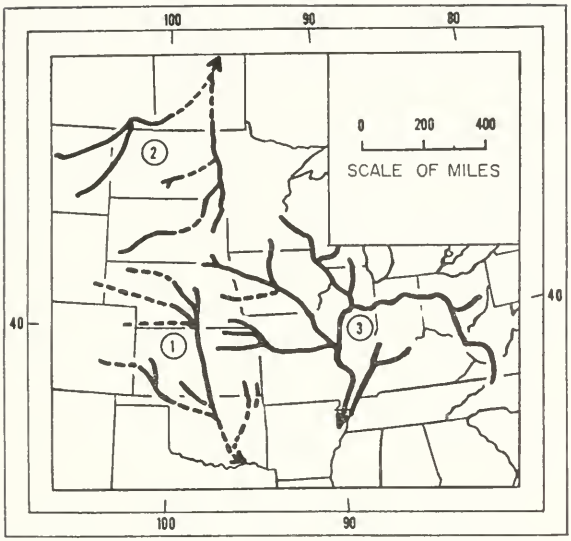

FIG. 3. Idealized preglacial drainage patterns in the central United States. Dotted lines represent hypothetical streamcourses; solid lines are based upon existing geologic information, but are, in part, also hypothetical. For sources see text. (1 = Drainage of Plains Stream System; 2 = Hudson Bay Drainage; 3 = Drainage of Teays/Mississippi System).

Evidence about the fauna of the Preglacial Plains Drainage (Fig. 3) can be derived from fossils found in beds of Pliocene age in the High Plains, and from climatic conditions that are thought to have existed then.

Hibbard (1960:11) pointed out that temperature and precipitation must be considered separately and not in terms of their present relationships in the Great Plains. He inferred, chiefly from paleontologic evidence, that in lower Pliocene time (p. 11) "The climate of the Interior Plains was mild-subtropical as far north and west as Shannon County, South Dakota" and that (p. 13-14) the early Middle Pliocene climate differed from that of the Lower Pliocene by a slight decrease in moisture. Hibbard characterized the Great Plains of the Lower Pliocene as (p. 13) ". . . a moist subhumid, subtropical, savanna with forests and tall grasses along the river valleys, with chiefly shrubs and tall grasses on the valley walls and on the low divides. Some short grasses may have occurred on the higher and well drained divides." In the Middle Pliocene he noted that there is evidence of large rivers having broad flood plains or

valleys with oxbow lakes in which diatomaceous marl was deposited. On the basis of fossil plant seeds and vertebrates found in Pliocene deposits in Beaver County, Oklahoma, Chaney and Elias (1936:34) visualized extensive grasslands or savannas in that area, during the Pliocene, traversed by streams with wooded valleys.

Leonard and Frye (1956:31) made a strong case for a gradual increase in aridity during the Pliocene of the Great Plains. This was substantiated by a decrease in numbers and ultimate disappearance in the fossil record of branchiate snails, the ascendancy of prairie grasses and the decrease of arboreal elements. In addition there were periods of caliche formation and a fining of sediments in the Late Pliocene, all of which suggested, according to these authors, a lowering of the water table.

A list of Pliocene fishes known from the High Plains has recently been compiled, augmented and discused by C. L. Smith (1962); only two of the species listed (*Ictalurus punctatus* and *Lepomis cyanellus*) are common in the High Plains Region today. The range of two other species (for which the fossil identification to species is indicated by Smith as doubtful) extends approximately to the eastern edge of the High Plains; these are *Ictiobus* cf. *bubalus* and *Aplodinotus* cf. *grunniens*. C. L. Smith (1962:512) suggested, with reservations, that *Fundulus detillai* Hibbard and Dunkle from the Middle Pliocene (Ogallala Formation) may be related to *Fundulus kansae*, a species now especially characteristic of streams of the High Plains. Recent counterparts of other species reported by Smith (1962) no longer occur naturally in the High Plains but are found farther to the east in the Mississippi Valley.

Despite the fragmentary nature of the fossil record of Pliocene fishes from the Great Plains, the known fauna (Hubbs, 1942:399; C. L. Smith, 1962:Table 1) indicates that catfishes of the genus *Ictalurus* and various sunfishes were probably common and that bowfin, gars, deep-bodied suckers, some cyprinids, cyprinodontids and an atherinid were present at one or more times. In North America today these groups, with the possible exception of the cyprinids, are best represented in the waters of the Atlantic and Gulf coastal plains and in the Mississippi Embayment. Hibbard's (1960) interpretation of Pliocene climate noted above suggests ecological conditions in which centrarchids, cyprinodontids, lepisosteids and large ictalurids might flourish if their ecological requirements approximated those observed for many members of these groups today.

Another line of evidence, indirect in nature, concerning the preglacial fauna of the present High Plains Region is offered by consideration of those species that now inhabit the western parts of the three rivers—Platte, Kansas and Arkansas—for which evidence best indicates preglacial interconnections (Fig. 3). Some of these connections continued into the Pleistocene until late Illinoian time or possibly somewhat later (Frye and Leonard, 1952:196-197). It is, however, difficult to ascertain which of the fishes now common to the three systems had their origin in the Preglacial Plains System, and which ones might more likely have reached the area after southward deflection of the Preglacial Hudson Bay Drainage (to be considered in a later section).

The zoogeographic importance of a Preglacial or Pleistocene interconnection of the western parts of the Arkansas, Kansas and Platte rivers was first suggested by Williams (1954:573) who theorized that the crayfish *Orconectes n. neglectus* dispersed into these systems by way of former stream connections west of the Flint Hills. D. A. Distler (personal communication) makes a similar case for dispersal of a subspecies of the orange-throated darter—*Etheostoma spectabile pulchellum*—via such connections. The native range of *E. s. pulchellum* extends from the Platte River southward to the Brazos and Colorado drainages of Texas, lending support to the view that the Preglacial Plains Drainage may have had connections to the south at one or more times in the past.

The distribution of the plains killifish, *Fundulus kansae,* coupled with that of the closely related (Miller, 1955:10, 11) or conspecific fish *Fundulus zebrinus,* resembles, in regard to stream systems involved, the distribution of *E. s. pulchellum,* except for the presence of the killifish in the Pecos River Drainage. Both *F. kansae* and *E. s. pulchellum* range from the Brazos and Colorado systems northward definitely as far as the Platte. There are scattered records of *F. kansae* north of the Platte, probably best attributed to introduction according to Miller (1955:11, 12). As noted above fossil evidence suggests that a progenitor of *F. kansae* inhabited the Preglacial Plains Stream.

The sucker-mouthed minnow *Phenacobius mirabilis* is found (disjunctly) in the Colorado River of Texas (Clark Hubbs, 1957: 93), and from the Red River northward to the Platte and some nearby drainages in northwestern Iowa and doubtfully in South Dakota (Bailey and Allum, 1962:54). The possible invasion eastward of this species from an area of origin in the Great Plains is discussed in the appropriate species account.

Several species depart from the pattern just discussed only in a greater degree of penetration northward. Two such species, *Hybognathus placitus* and *Notropis l. lutrensis,* are, in the main, trans-mississippian in distribution. Three others, *Carpiodes c. carpio, Lepomis cyanellus* and *L. humilis,* now range farther east but reasons for suspecting a western origin are presented in the accounts of these species.

The western subspecies of the sand shiner (*Notropis stramineus missuriensis*) occurs from the upper Missouri River Basin southward to the Arkansas River System and there is evidence of intergradation between this subspecies and another, eastern subspecies in the western part of the Red River System in Oklahoma.

The range of the southwestern subspecies of the flat-headed chub (*Hybopsis gracilis gulonella*) does not extend so far south as the Red River but does include the Arkansas River System and the upper Pecos Drainage and the western part of the Missouri River Drainage. (Possibly stocks of this fish were extirpated in the Red River and other rivers to the south that lack mountain-headwaters during dry periods in the past such as the one suggested by Frye and Leonard [1963:19] for the upper part of the Red River Basin in Illinoian time.)

Notropis topeka ranges from the Arkansas River northward to the Missouri River (Bailey and Allum, 1962:Fig. 6). This species probably inhabited the Preglacial or Pleistocene Plains Stream and in post-glacial time extended its range into Minnesota, Iowa and Missouri. The southwestern limits of the range of the Topeka shiner seem to be retreating northeastward; *N. topeka* is now rare or absent west of the Flint Hills in the Arkansas and Kansas river systems, although it seemingly was common there in historic time (Minckley and Cross, 1959:210-211).

Possibly there has been widespread extirpation of southern populations of *Fundulus sciadicus,* which seems also to have originated in the Preglacial Plains Stream or the Preglacial Missouri System, judging from its western distribution at present.

A number of other species are wide-ranging in the Mississippi Valley and their areas of origin are obscure; however, they probably inhabited the Preglacial Plains Stream (as well as other ancient drainages) because:

(1) they are widespread in southwestern stream systems, including the Pecos System;

(2) southwestern or western populations differ morphologically from eastern populations, suggesting a long sojourn there rather than recent invasion.

Species meeting one or both of these specifications are: *Hybopsis aestivalis, Semotilus atromaculatus, Pimephales promelas, Campostoma anomalum, Carpiodes cyprinus, Catostomus commersoni* and *Ictalurus melas.* Also deserving mention here are *Notropis atherinoides,* western representatives of which have, until recently (Bailey and Allum, 1962:56-60), been deemed specifically distinct, and *Notropis blennius,* for which a southwestern subspecies has been recognized by Hubbs and Bonham (1951:103).

HUDSON BAY COMPONENT

Former outflow of parts of the upper Missouri River System to Hudson Bay was suggested by Todd (1914, 1923), Flint (1955:148, 1957:Fig. 10-2), Horberg and Anderson (1956:106) and Meneley, Christiansen and Kupsch (1957). Todd inferred a pre-Nebraskan, northward drainage of Missouri River tributaries as far south as the White River in South Dakota (1914:267). Flint (1955:148) suggested that a drainageway, at least as old as pre-Illinoian, comprising Cheyenne, Grand and Moreau rivers, led north from northeastern South Dakota into the Hudson Bay Drainage. The evidence consists of high-level abandoned valleys and areas of collapsed glacial drift east of the present Missouri River in South Dakota. Flint interpreted the northern point of the Coteau des Prairies as a headland between the "Ancient Cheyenne" mentioned above and the "Ancient Minnesota"—these two streams having their confluence north of this headland and proceeding thence to an Arctic egress (Fig. 3). In a study of bedrock topography, Meneley, Christiansen and Kupsch (1957) found evidence of a "Pre-glacial Missouri" that trended northeastward from the vicinity of Poplar, Montana, across the northwestern corner of North Dakota into Saskatchewan where it was joined by a "Preglacial Yellowstone," also trending northeastward from the area of present Williston, North Dakota. Together these streams coursed eastward across southern Saskatchewan into Manitoba where they joined a "Preglacial Red River" and then proceeded northward to the present region of Hudson Bay (Fig. 3).

Evidence indicates, then, that the Preglacial Missouri System was a major waterway draining, in the United States, a large area including parts of Montana, Wyoming, North and South Dakota, Minnesota, and possibly other areas to the east.

There is little published evidence concerning the fishes that in-

habited the Preglacial Hudson Bay Drainage and the extent to which its fauna differed from faunas of the Preglacial Plains Stream System and the Preglacial Teays/Mississippi System.

Deflection Southward of Ancestral Missouri System

One can reasonably assume (as did Alden, 1924:413) that in the northern Great Plains during Pleistocene glaciation, water must have escaped to the south, west of the glaciers, (Fig. 4) granted, of course, that small amounts of water may have escaped supra-glacially, intraglacially or percolated through gravels under the glaciers (Flint, 1957:158-159). During each of the glacial maxima water from the Upper Missouri Region was occluded from flowing northward to Hudson Bay, a region considered (Flint, 1957:316-318) to have become glaciated early in all glacial ages. Connections to the Hudson Bay Drainage would seem to have been in preglacial times or during interglacial stages.

Widespread and thick accumulations of Holdrege gravels in Nebraska (Lugn, 1935) suggest a great inflow of glacial water into that state from north and west during Nebraskan glaciation. At the time of the Kansan glacial maximum, drainage from a vast area of the northern Great Plains, between the glacial front and the Rocky Mountains, must have been funneled south into and across Nebraska (Fig. 4). It is, then, not surprising that massive gravel and sand deposits, of the magnitude of the Grand Island Member, were deposited in central Nebraska in Kansan time. Lugn (1935:117) stated in reference to the Holdrege and Grand Island gravels, "The thickest fluviatile deposits occur in the counties west of the till border, where the Missouri-Niobrara drainage flowed southward along the ice margins . . ." Lugn (1935:168) also considered the ancestral North Platte River an important bearer, in Kansan time, of water and sediment from part of the High Plains and Rocky Mountains. He thought that much of the Grand Island inwash sediment in south-central Nebraska was borne by the ancestral North Platte.

South of Nebraska during the Kansan maximum, water must have flowed south, west of the glacial ice and the Flint Hills, approximately along the course of the long-used master-stream of Pliocene antecedents through the Pleistocene McPherson Valley and southward at least as far as the Ancestral Arkansas River Drainage (Fig. 4). This view has been taken by Lohman and Frye (1940:852) and Frye and Leonard (1952:190, 191), chiefly

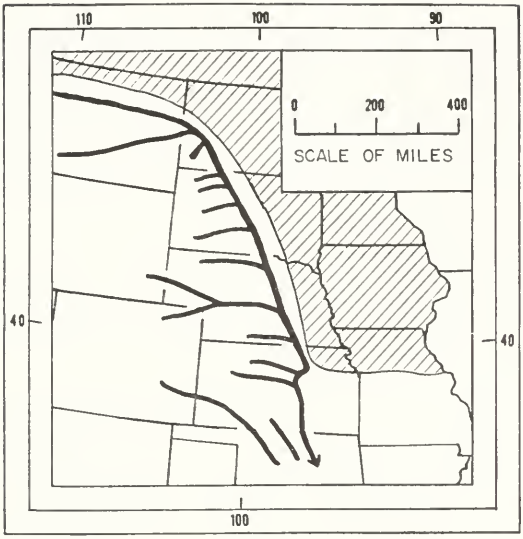

FIG. 4. Drainage pattern of the Ancestral Plains Stream System as it may have been at the time of maximum extent of the Kansan Glacier.

from the presence of sediments interpreted as glacial outwash from the northeast in McPherson Channel. However, Bayne and Fent (1963:372) recognized no outlet of Kansan glacial meltwaters to the southwest and considered drainage of the Solomon River area to have been to the east through the Flint Hills throughout Pleistocene time (p. 367). This interpretation of an early Pleistocene through-flowing Kansas River seems not to be borne out by the studies of gravel lithology reported by Davis (1951:183-189).

As north-flowing streams of the Ancestral Missouri System were deflected southward by encroaching glaciers, fishes indigenous to the area probably were also deflected southward. It could, of course, be argued that climatic conditions in advance of the oncoming glaciers were so severe, or glacial advance so rapid, that aquatic life in the upper Missouri was extirpated. This view seems extreme, however, as several authors have presented evidence that climatic effects on the biota, even a few miles in advance of the glaciers, did not result in a general extinction. Hibbard (1960:20, 21) suggested that during late Kansan time southwestern Kansas enjoyed a more equable and/or warmer climate than today. Frye and Leonard (1952:161) inferred that western Kansas had more rainfall, a slightly lower mean temperature, and more equable

temperatures during late Kansan time that at present. They noted that occurrences of fossil gastropods suggested presence of more permanent waters and woodlands that at present, but indicated no widespread forests. Deevey (1949:1394), in discussing the repopulating of deglaciating areas by aquatic animals, concluded that streams carrying glacial meltwater were not excessively cold and that the glacial lakes, though colder than their descendants today, were not arctic.

Thienemann (1950:335) noted that the central European aquatic fauna, even when compressed in a region of tundra between northern and Alpine glaciers, contained species still found in the same region.

It seems likely, then, that faunal components of the Preglacial Missouri River System did not suffer extinction but persisted locally and were brought into contact with stream systems to the south. These may have included the western headwaters of some streams of the Teays/Mississippi System (Fig. 3). Horberg and Anderson (1956:Fig. 2), for instance, have tentatively mapped the headwaters of some streams of an Ancient Iowa River System and some other tributaries of the Teays/Mississippi as extending west into the Great Plains. (I have pointed out above that western tributaries of the Ancient Platte more likely flowed southward into the Preglacial Plains Stream.) It seems that the upper Missouri and other streams heading west of the glacial fronts of the Nebraskan and Kansan advances were deflected into the south-flowing Plains Stream west of the Flint Hills in Kansas (Fig. 4). Thus the first and second and possibly later glaciers probably caused a mingling of stocks of the Preglacial Missouri and Preglacial Plains Stream and possibly a lesser mingling with stocks of some western headwaters of the Teays/Mississippi. Bailey and Allum (1962:120) listed six kinds of fishes (*Semotilus margarita nachtriebi, Chrosomus neogaeus, C. eos, Hybopsis plumbea, Catostomus catostomus* and *Pantosteus platyrhynchus*) that they believed capable of enduring the last glaciation(s) in the upper Missouri in South Dakota. I suspect that several other species, originally derived from the Preglacial Missouri System or from western tributaries of the Teays/Mississippi System, persisted in the Middle or Upper Missouri during the Pleistocene for the following reasons:

(1) Certain species exhibit racial variation from north to south in the Missouri System. These differences may be residual evidence of originally different races in the Preglacial Missouri and Preglacial Plains drainages. The existence of such differences argues for a northwestern origin rather than colonization in post-

glacial times from a southeastern source in the lower Missouri River Basin. Penetration after the last glacial advance into the middle Missouri River Basin by way of connections to the upper Mississippi River System has been suggested for several species of fishes in eastern South Dakota by Bailey and Allum (1962:122). However, most of the fishes so categorized by Bailey and Allum seem localized east of the Missouri River. The species treated here are not so localized. Probably they endured at least one glacial advance in the upper and middle Missouri River Basin.

(2) The species to which my argument pertains are widespread in Canada, at least as far north as Hudson Bay, and also penetrate west into the cooler headwaters of the Missouri System in Wyoming and central Montana. Species possessing a tolerance that has enabled their dispersal far northward might have survived Pleistocene conditions in the area of the present Upper Missouri Basin. Certain fishes of present-day northern affinities may, in Pliocene time, have existed in the Hudson Bay and other Arctic drainages of Canada.

Species that are in accord with both criteria mentioned above are *Catostomus commersoni, Pimephales promelas, Moxostoma macrolepidotum* and *Hybopsis gracilis.* The three species listed first or their progenitors could have inhabited all three preglacial drainages treated here, in view of their present wide ranges. *Hybopsis gracilis* may have inhabited only the Preglacial Missouri and the Preglacial Plains Stream drainages.

Other species, occurring at present in the Missouri River System, meeting the second criterion above, and considered likely inhabitants of a Preglacial Missouri System are: *Hiodon alosoides, Rhinichthys cataractae, Notropis atherinoides, Percopsis omiscomaycus, Culaea inconstans, Notropis heterolepis* and *Lota lota.*

The virtual restriction of *Scaphirhynchus album, Hybopsis gelida,* and *Hybopsis meeki* to the Missouri River System suggests an origin for these species in the Preglacial Missouri System.

MISSISSIPPI COMPONENT

Probably the easternmost part of the Kansas River System, east of the Flint Hills, long flowed to the east (Frye and Leonard, 1952:185) and was a part of the Preglacial Teays/Mississippi System (Fig. 3), whereas the western part of the system flowed south, west of the Flint Hills, through the time of Kansan glaciation. Because the Kansan glacier overrode most of the present Kansas River Basin east of the Flint Hills, repopulation from the

east must have taken place during glacial retreat or thereafter. After this retreat, capture of streams progressing farther westward, incorporated several tributaries of the Plains Stream into the Kansas River system, culminating in a drainage pattern closely resembling that of the present (Frye and Leonard, 1952:193-196).

Downcutting westward in mid-Pleistocene time has been documented for the Kansas River (Frye and Leonard, 1952:192ff.) at a time (Illinoian and/or during the preceding or succeeding interglacial ages) when the Ancestral Plains Stream, flowing south through McPherson Channel in central Kansas, was aggrading its channel. Ultimately the south-flowing stream proved unable to hold its own against the vigorous invader from the east. Frye and Leonard (1952:193) attributed this piracy mainly to isostatic readjustments.

Quinn's (1958:42) evidence, although scant, indicated a similar westward cutting through an Ozark/Ouachita Highland by a tributary of the Mississippi, the Ancestral Arkansas River, to capture another segment of the Plains Stream System.

In regard to deflection eastward of the Platte, Lueninghoener (1947:60) wrote, "It seems reasonable to visualize the initial erosion of the Platte River Valley to have taken place in Yarmouth time by a Missouri River tributary eroding headwardly across the till border. Headward erosion appears to have progressed until capture of some of the drainages west of the till border took place." Lugn (1935:153) wrote, "A long time must have elapsed before the drainage west of the till border . . . was captured and diverted through the new post-Loveland Platte River."

All these instances suggest that downcutting westward by streams of the Mississippi System occurred in the mid-Pleistocene, subsequent to Kansan glaciation, in Yarmouthian or Illinoian time. This rough correspondence in time of deflection of several stream systems may be fortuitous, may be related to isostatic changes in the region, or may reflect a widespread pattern of climatic change. A primarily climatic mechanism whereby a south-flowing Plains Stream might have been captured, segment by segment, by east-flowing tributaries of the Mississippi System is suggested by reports (Frye and Leonard, 1952:165; 1957:29; 1963:19) of the onset of widespread aridity in the High Plains, especially to the southwest, in Illinoian and/or Yarmouthian time. These writers (1952:165) stated, "It is difficult to escape the conclusion that a profound change in ecological conditions in the Great Plains occurred during or at the close of the Yarmouthian interglacial interval, or at the

beginning of the Illinoian cycle of erosion and deposition. Wholesale extinction of great populations of branchiate and other gastropods adapted to life in permanent water, which thrived in western Kansas in late Kansan and early Yarmouthian time, is indicative of a less humid environment, or at least of a marked decline in the prevalence of permanent ponds and lakes of clear water in the Great Plains region." These authors further stated (p. 165) ". . . the aquatic gastropods in Illinoian deposits indicate an environment of ephemeral ponds and silt-laden streams." The effect of such a climatic change on streams of the High Plains is further suggested by their description (Frye and Leonard, 1957:29) of conditions in the High Plains of Texas in Yarmouthian and Illinoian time. They wrote that streams were less competent in these Ages than in either the Kansan or Early Wisconsinan and that there may have been reduction of topographic relief due to the choking of minor valleys with sediments that streams were not able to carry away. The south-flowing Ancestral Plains Stream, entering and attempting to cross an arid or semi-arid region such as the one just described, might, in accordance with the principles discussed by Quinn (1957:156), have deposited its load and aggraded its channel as its waters evaporated. Such a choked, meandering stream might have been captured by tributaries of the Mississippi as they, debouching in an area of higher rainfall, cut westward relatively rapidly.

The entire Kansas River System, then, eventually had its outlet into the Mississippi River. This provided access to the entire newly-integrated system of an eastern fauna. An earlier faunal contribution (discussed above) to the Ancestral Plains Stream from the Ancestral Teays/Mississippi might have been incorporated from tributaries of the Mississippi (for example, the Ancestral Des Moines River) that were deflected southward due to encroaching glaciers of the Nebraskan and Kansan advances.

Many species, typical of the larger rivers of the Mississippi Valley, must have made their way up the major watercourses of the Missouri System, including the lower part of the Kansas River and its larger tributaries. Evidence as to which of the big-river fishes first reached the Kansas River Basin from this source is scant. The former distributions and area of origin are difficult to judge for species that now inhabit the mainstreams of large rivers, because: (1) after confluence of formerly disjunct drainages, barriers to dispersal of such fishes seem nonexistent; (2) thus, formerly allopatric species may soon occupy almost wholly sympatric ranges;

(3) mingling of stocks may be so nearly complete, due to the relatively large size and high vagility of some big-river species, that any racial differences that may have existed soon disappear. Thus, less insight into their geographic history seems possible than in the case of upland species that inhabit peripheral waters of a major drainage basin. Consequently, big-river fishes probably have a lesser tendency and opportunity for speciation than do small-stream fishes.

Underhill and Merrell (1959:140) theorized that intrabasinal variation in *Notropis dorsalis* is partly attributable to preference of this species for small streams where populations become isolated to some extent; the larger, more turbid intervening streams are thought to act as a barrier between populations in the tributaries. Neighboring, but unconnected stream systems may have many "large-river-species" in common. Thus, some species characteristic of large rivers, entering the Kansas River System from the east after retreat of the Kansan Glacier and downcutting westward into the Plains Stream System, probably encountered and mingled with populations of the same or closely related kinds that already inhabited the Plains Stream. C. L. Smith (1962) reported genera typical of larger rivers in some Pliocene faunas found in the High Plains (*Lepisosteus, Ictiobus, Ictalurus, Aplodinotus*? and *Pomoxis*). Some of these as well as other genera typical of larger waters have also been reported by C. L. Smith (1954, 1958) and G. R. Smith (1963) from beds of mid-Pleistocene age—all of which suggests a long sojourn in the central United States for many big-river fishes.

In the case of several small (and possibly less vagile) cyprinids that occupy large rivers, mingling has not so completely erased differences between eastern and western populations. This is especially true of *Notropis stramineus,* which occurs in small as well as in large streams. In *Notropis atherinoides, Notropis blennius,* and *Hybopsis aestivalis* the evidence of mingling with eastern stocks seems stronger in the Kansas River Basin than in the Arkansas River Basin and other stream systems to the south.

Species of the Kansas River Basin clearly tolerant of larger rivers and, in many cases, restricted to them and seeming to have had an eastern, or a mixed origin include:

Ichthyomyzon castaneus
Scaphirhynchus platorynchus
Polyodon spathula
Lepisosteus platostomus
Lepisosteus osseus
Dorosoma cepedianum
Cycleptus elongatus
Ictiobus cyprinellus
Ictiobus bubalus
Ictiobus niger
Ictalurus punctatus
Pylodictis olivaris

Hybopsis storeriana
Notropis atherinoides
Notropis blennius
Notropis buchanani
Notropis stramineus
Notropis shumardi
Anguilla rostrata
Pomoxis annularis
Stizostedion canadense
Stizostedion vitreum
Aplodinotus grunniens
Roccus chrysops
Hybognathus nuchalis

Bailey and Allum (1962:121) described a category of fishes, which, like that above, probably entered South Dakota from the southeast by way of the Missouri River but which consisted of species more typical of upland creeks than of large and often turbid rivers. Species, so characterizable, also undoubtedly entered the Kansas River Basin from the east. Conditions for invasion by kinds that prefer clear water of upland tributaries likely were favorable in the interval following retreat of the Kansan glacier and before extensive downcutting westward had taken place (while the river headed east of the Flint Hills). The lower mainstream presumably was clearer than at present and probably possessed rubbly and gravelly bottoms with frequent riffles, as do the present Neosho and Verdigris rivers that head mainly in the Flint Hills. As discussed by Bailey and Allum (1962:122), upland fishes possibly venture into large rivers when they are clear and cool, as in winter. Some species may, even under present conditions, ascend stepwise from one year-round habitable tributary to the next by a process here termed "tributary-hopping."

Especially important as a source-area for upland fishes was the rich faunal area of the Ozark Plateau, the northwestern limits of which are within 100 miles of the mouth of the Kansas River. Several upland species of Ozarkian affinities are, at present, restricted to the clearest and least-modified streams of both the Kansas and Arkansas river systems.

Like the species typical of large rivers, some species that are typical of upland streams may have met and mingled with closely related populations already inhabiting the western part of the Kansas River Basin. (Species thought certainly to have inhabited the Ancestral Plains Stream are indicated by asterisks in the list below.) The populations of these species now present in the Kansas River possibly were derived from all three preglacial stream systems (Fig. 3). Following is a list of kinds that now occupy upland tributaries in the Kansas River Basin, and that probably entered the Basin from the east. In the case of *Moxostoma macrolepidotum* and *Etheostoma spectabile* the eastern influence is detectable only through the presence of intergrading subspecies.

Carpiodes velifer
* *Catostomus commersoni*
Moxostoma erythrurum
Moxostoma macrolepidotum
Chrosomus erythrogaster
Hybopsis biguttata
Notropis cornutus
Notropis dorsalis
Notemigonus crysoleucas
Notropis rubellus
Notropis umbratilis
Pimephales notatus
* *Semotilus atromaculatus*
* *Ictalurus melas*
Ictalurus natalis
Noturus exilis
Noturus flavus
Etheostoma nigrum nigrum
Percina caprodes
Percina maculata
Micropterus salmoides
Lepomis macrochirus
Lepomis megalotis
* *Etheostoma spectabile*
* *Pimephales promelas*

Along with fishes, the aquatic snails *Campeloma subsolidum* (Anthony) (Leonard, 1959:31), *Pleurocera acuta* Raf. (Goodrich, 1939:4), and the crayfish *Orconectes luteus* (Creaser) (Metcalf and Distler, 1961:354) probably entered the Basin from the east. The snails are, at present, presumably extinct in the Basin.

Several of the species listed probably entered the Kansas River Basin solely from the east after retreat of the Kansan Glacier. In this category would seem to belong those species that presently occur in the Kansas River System but not in the Arkansas River System—thus suggesting arrival in the Kansas River Basin too late to utilize the McPherson Channel Connection to the Arkansas River. Although the Arkansas River also came ultimately to flow into the Mississippi River (in post-Pliocene, but pre-Sangamonian time according to Quinn, 1958:42), its connections were far south of those of the Kansas River and thus introduced into the Arkansas River System a somewhat different fauna with more southern affinities. Species or subspecies that occur in the Kansas River System but not in the middle and upper Arkansas River System are few in number and include *Hybognathus hankinsoni, Hybopsis aestivalis hyostoma, Notropis cornutus, Notropis dorsalis, Lota lota, Hybopsis gelida, Hybopsis meeki, Scaphirhynchus albus,* and *Hybopsis gracilis: gracilis* x *gulonella* (only *H. g. gulonella* occurs in the Arkansas System). *H. g. gracilis, H. gelida, H. meeki* and *S. albus* are not found anywhere outside the Missouri River System and that part of the Mississippi River near and downstream from the mouth of the Missouri. As suggested elsewhere, these seem to be old, endemic fishes of the Missouri River, derived from the preglacial north-flowing Missouri rather than from an eastern source.

Diversion to the east also opened pathways of dispersal for fishes originating in the Great Plains. Kinds that have invaded eastward from a probable Plains source include *Carpiodes carpio*

carpio, Notropis l. lutrensis, Notropis topeka, Phenacobius mirabilis, Hybognathus placitus, Campostoma anomalum pullum, Fundulus kansae, Fundulus sciadicus, Lepomis cyanellus, and *Lepomis humilis.* Gene flow from western populations is detectable in populations of *Notropis stramineus* and *Etheostoma spectabile* east of the mouth of the Kansas River in Missouri.

VARIATION FROM NORTHEAST TO SOUTHWEST

As the Preglacial (north-flowing) Missouri River System was deflected southward (possibly incorporating some western tributaries of the Teays/Mississippi System) into the Ancestral Plains Stream, faunal elements were probably concomitantly deflected, resulting in a mingling of stocks. At least one mingling of eastern and western stocks occurred after deflection of some sections of the Plains Stream eastward. Probably other deflections with faunal mixing took place in glaciated areas and glacial fringe areas of the central United States outside the region considered here.

To what extent, if any, northern connections to Hudson Bay may have been renewed during interglacial stages is not known. However, at the present time, approximately 11,000 years (Frye and Willman, 1960:Fig. 1) since the Valderan glacial advance, streams tributary to Hudson Bay already have penetrated as far south as South Dakota. Surely during interglacial stages stocks must have met and mingled as they repopulated large sections of deglaciating terrain in Canada and the northern United States.

Throughout the Pleistocene there probably was little opportunity for extended periods of isolation—and, in consequence, little impetus to speciation—in areas of plainlike topography that were repeatedly glaciated or that were immediately adjacent to glaciers. In such areas repeated glacial retreat and advance probably furthered renewed intermingling of stocks rather than isolation of stocks with possible subsequent speciation. On the other hand, in regions where glaciers abutted areas of broken topography (for example the northern Appalachian Mountains and Cumberland and Ozark Plateaus) isolating mechanisms might have been strengthened by encroachment and retreat of glaciers. Probably also in nonglaciated areas in the southwestern United States Pleistocene climatic fluctuations enhanced the process of speciation, whereas in glaciated areas of the Great Plains and Interior Lowlands climatic fluctuations inhibited the process. Thus, as pointed out by Grinnell (1924:228) and Miller (1948:128), arid regions have produced,

through a process of isolation, new kinds, both of terrestrial and of aquatic animals. On the other hand, Thienemann (1950:390) wrote of a *"Glaziale Mischfauna"* produced by encroachment of glaciers on the plains of Central Europe noting (p. 336) that resistant remnants of the preglacial, middle European fauna became mixed with immigrants from the Alpine and Polar regions.

Within the present Mississippi River System, southwestern variants of some fishes have been given taxonomic recognition as subspecies or as species having sibling species to the northeast. In these fishes, characters vary in the same manner in a southwesterly direction. Some kinds of variation, together with examples, are listed below. ("Northeastern" here refers to populations from the Ohio River System and upper Mississippi River System. "Southwestern" refers to the upper Arkansas River system, the upper Pecos River Drainage, and the upper Red River of the South. Intervening waters show various kinds and degrees of intergradation.)

General Body Shape

Northeastern representative of the fishes considered here tend to be fusiform in body outline. Dorsal and ventral profiles curve smoothly and slightly anteriorly and posteriorly from the point of greatest body depth near the midpoint of total body length. The body is slender, the ratio of greatest body depth and head depth to standard length being less than in southwestern fishes. The smooth, slight degree of curvature continues along dorsal and ventral head profiles resulting in an acute, tapering snout, terminating approximately midway of the vertical distance between the top and the bottom of the head. The head is usually small in relation to the entire body—frequently being shorter, narrower and shallower than in southwestern kinds.

Southwestern fishes tend to be chubbier in body form, especially anteriorly. The point of greatest body depth is generally anterior to the mid-point of total length. From this point there is a striking decurvature of the anterior dorsal profile resulting in a "humpbacked" appearance. The posterior dorsal profile descends more gradually than the anterior to the caudal peduncle, which is generally only slightly deeper than the peduncle of northeastern fishes. The total impression is of a chubby fish, thick-bodied anteriorly, and tapering to a slender caudal peduncle. The head is relatively larger in southwestern kinds, generally being wider, deeper, longer and more massive. This may be in keeping with Hubbs' (1940b:

199) observation that fish in warmer waters typically have deeper bodies and larger heads than those of colder waters. As pointed out elsewhere, however, higher altitudes may, in the western parts of most of these southwestern streams, produce cold water temperatures. In southwestern kinds the snout is blunter and the ventral contour of the head is less upcurved than in northeastern kinds. Lines connecting (a) the occiput, (b) the ventral surface of the head directly below the occiput and (c) the anteriormost terminus of the snout tend to form a right triangle in southwestern fishes, in northeastern fishes such lines tend to form an isosceles triangle. Olund and Cross (1961:333), in comparing heads of a southwestern subspecies, *Hybopsis gracilis gulonella,* and a more northern subspecies, *H. g. gracilis,* found the former to be rounded anteriorly (decurved) in side view and deeper, whereas the latter was wedge-shaped in profile and much shallower. Probably the most extreme example of pronounced anterior decurvature to the southwest is found in the chub *Hybopsis aestivalis* as represented in the Arkansas and Red rivers (*H. a. tetranemus* and *H. a. australis* respectively). The minnow *Pimephales promelas* and several of the species of *Notropis* also exhibit anterior decurvature especially well (for example southwestern as contrasted with northeastern populations of *N. blennius* and *N. stramineus.*) This condition has been pointed out by Hubbs and Bonham (1951:103-107) in *N. blennius. Hybognathus nuchalis* from the northeast and its sibling species *Hybognathus placitus* from the southwest show a similar difference in body shape. This variance is also observed where these two species are sympatric in the lower Kansas River Basin.

As concerns other than cyprinid fishes similar tendencies in body shape were observed in the sucker *Catostomus commersoni.* Hubbs and Black (1940:227) noted that in the southwestern subspecies of the carpsucker *Carpiodes carpio*—called *elongatus*—the anterior part of the back is more arched than in the northern subspecies—*carpio.* The darter *Etheostoma spectabile* comprises, among others, a plains subspecies (*E. s. pulchellum*) with an arched and decurved anterior profile, whereas the typical subspecies, ranging from the northern Ozarks eastward, exhibits a more fusiform body profile. The same differences in profile were noted between *Etheostoma cragini* of the central and western Arkansas River Basin and *Etheostoma pallididorsum* of the Caddo River Drainage in Arkansas (Distler and Metcalf, 1962:Table 2).

Mouth

In correlation with the decurved snout of southwestern representatives the mouth tends to be less nearly terminal and more nearly horizontal, and that of northeastern fishes in more nearly terminal and is oblique. This is especially true of *Pimephales promelas* from northeast to southwest (Taylor, 1954:42; Hubbs and Ortenburger, 1929a:38). In the species *Notropis blennius* northeastern populations characteristically possess an oblique, terminal mouth, whereas southwestern populations tend to have a more inferior, horizontal mouth. *Hybopsis gracilis, Rhinichthys cataractae, Notropis stramineus* and *Campostoma anomalum,* on the other hand, show little variation as regards this character, having inferior, horizontal mouths throughout their range.

Eye

Hubbs (1940b:202) and Bailey (1956:333) pointed out that eye size tends to be smaller in plains representatives of some species of fish. Moore (1950) noted this in several members of the genus *Hybopsis* that inhabit plains streams. The reason for the smaller eye of Plains minnows is not entirely clear. Moore (1950:92) suggested that in some species smallness was related to decreased light in turbid waters of Plains streams and to the greater development of cutaneous sensory structures. That there is a selective value in some degree of reduction in the amount of eye surface exposed in sandy streams of the Great Plains is suggested by study of populations of *Semotilus atromaculatus* from shallow, sandy streams of the western Platte and Kansas river systems. In these fish there is, in addition to a smaller eye than in eastern populations (Table 8), a partial overgrowth of skin around the periphery of the eye, further decreasing the surface area exposed. *Notropis atherinoides* from the Kansas River also exhibits peripheral overgrowth of skin around the eye and partial overgrowth of skin was pointed out by Moore (1950:92) for the eye of the chub *Hybopsis meeki.*

Scales

Many species of fishes have smaller scales in the Missouri River and other Plains streams than in the Ohio and upper Mississippi basins (see Bailey, 1956:333). For the sand shiner, *Notropis stramineus,* Bailey and Allum (1962:Table 5) presented data showing higher counts of body-circumference scales toward the west. Sev-

eral comparisons reported on herein show a comparable tendency. In most species inhabiting the Great Plains sections of the Platte, Kansas, and Arkansas rivers, further smoothing of the external surface seems to be achieved by embedding of scales, especially the ventral and predorsal scales. In *Notropis dorsalis* of the western Platte (*piptolepis* of some authors) and in occasional specimens of *Notropis stramineus*, reduction in scale size and embedding have resulted in a predorsum naked in appearance.

Adaptive Value

A number of features have been noted that, to a greater or lesser degree, characterize southwestern races of some wide-ranging fishes. These have included decurved anterior dorsal profile, inferior, horizontal mouth and small eyes and scales. In some western fishes of turbid rivers there has been a marked development of cutaneous sense organs on the lower surface of the body and of barbels around the mouth. These features last-mentioned are probably adaptive and may (Moore, 1950:91-92) afford the fish greater cognizance of the substrate. Additional adaptive values were suggested by Hubbs and Walker (1942:101, 102), who in regard to certain psammophilous shiners wrote: "In correlation with their life on the open bottom in the current, they have terete bodies, with the dorsal contour more strongly arched than the ventral. The pectoral fins are large and horizontally expanded. The snout is long and decurved, and the large mouth in inferior. These morphological features adapt the fish to swimming about and feeding over the open bottom, in the current. The form of the head, body and fins is such as to increase the downward component of the force of the current, so as to help hold the fish against the bottom." Hubbs (1940:200) suggested that smaller scales provide a smoother surface that might be advantageous in facing the stress of water currents.

Variation, Its Possible Causes and Its Taxonomic Interpretation

The interpretation of the variation existing from northeast to southwest in terms of taxonomic treatment has been diverse.

Southwestern or western (Great Plains) populations of the several species involved have been considered variously as (1) specifically distinct, (2) subspecifically distinct or (3) not taxonomically distinct—from eastern or northeastern populations of the

Mississippi Valley. In the course of time some kinds have been placed by various workers in more than one of the categories just mentioned.

This lack of consistency in taxonomic treatment suggests the complex nature of the problems that these fishes present and intimates that in some cases differences are more easily observed than in others. Despite this complexity there is among the various kinds of fishes concerned some concordance (as pointed out above) in regard to characters involved and in the clinal expression of these characters from east to west or northeast to southwest. Bailey (1956:334) suggested this in writing, "It is of interest to note that where . . . Mississippi basin fishes have intimately related species or subspecies on the Great Plains, the same character differences are usually involved." Bailey specifically mentioned the smaller eye and greater number of circumferential body scales found in populations from the Great Plains.

The problem arises whether this difference is purely a phenotypic response made during ontogeny to an environmental stimulus or is the expression of a genotype of wide occurrence in streams of the areas involved. Studies by several investigators have demonstrated the modifiability of the phenotype of some fishes experimentally by certain environmental stimuli. Bailey and Gosline (1955), Needham and Gard (1959), Underhill and Merrell (1959), Olund and Cross (1961), Strawn (1961), and Barlow (1961) have listed many of these studies and summarized important aspects applicable here. Several authors (Bailey, 1956:333-334; Bailey, Winn and Smith, 1954:149, and Strawn, 1961:155) have suggested that some phenotypic variation observed in natural populations may also be a direct result of environmental stimuli such as temperature, chemical content of water, light or diet. On the other hand, Lagler and Bailey (1947:58) provided experimental evidence for the genetic fixity of degree of squamation in two subspecies of *Etheostoma nigrum*. Heuts (1947:100-102) found fresh and saltwater races of *Gasterosteus aculeatus* to be genetically distinct. D. A. Distler (personal communication) reared stocks of four geographic races of the darter *Etheostoma spectabile* for several generations under laboratory conditions as nearly identical as possible. No phenotypic differences were observed that would have made identification to subspecies any more difficult for F_1 or F_2 progeny than for the respective parental stocks.

In characters of Plains fishes that are most likely of adaptive value it seems unwarranted to attribute great significance to direct environmental stimulus. There seems to be no reason to think that a character of advantage to the organism would necessarily be consistently produced by direct stimulus from the environment during an early developmental stage. Such an advantageous response to environmental stimulus, where and if it occurs, probably is fortuitous. If advantageous modifications could be attained simply by direct environmental stimulus there would be little need for genotypic change (allowing for speciation) to take place.

Hubbs (1943:118) noted that a majority of the taxonomic characters employed in racial analysis of fishes behaved according to a Galtonian type of inheritance—that is to say, in a manner best explained as being controlled by multiple factors. Underhill and Merrell (1959:144-145) pointed out that certain meristic characters such as anal rays may be remarkably stable within a population, whereas other characters may exhibit much variation from population to population. They suggested that these variable characters might be controlled by multiple genes. Needham and Gard (1959: 76) postulated that multiple genes may control the migratory instinct in the rainbow trout, which shows various gradations of development. The broad "normal curves" obtained from analysis of various body proportions and of some meristic characters of Plains fishes suggests control by multiple genes. If control of such characters is rather by direct environmental stimulus the results seem, in any event, to be indistinguishable.

Underhill and Merrell (1959:145) speculated that genotype may simply determine the upper and lower limits of variation in regard to highly variable meristic characters. They further suggested that environment "operates on the existing genotypes, modifying their expression within their reaction ranges and also selecting the better adapted genotypes." Needham and Gard (1959:75) termed such environmental effects as "direct" and "selective." Both (a) the ability of the organism to adapt to the environment and (b) its limits of modifiability during development would seem to be ultimately under genic control.

The relationships discussed in the preceding paragraphs might be summarized thus: the genotype attained through natural selection produces a phenotype that is adaptive and, in addition, determines the limits to which this phenotype can be modified directly by the

environment. Direct stimulus seemingly could produce a phenotype that is adaptive (and thus additive to the process of natural selection), neutral, or even non-adaptive.

Thus, evidence seems great as pointed out by Miller (1948:148, 1961:555), Bailey and Gosline (1955:24), Needham and Gard (1959:73, 77), Underhill and Merrell (1959:145), Olund and Cross (1961:342) and Strawn (1961:155) that the phenotype observed (and which must be dealt with taxonomically) is the product both of heredity and of direct environmental stimulus. Strawn (1961: 155) termed this relationship the "product of a given environment interacting on the genotype."

For fishes of the Great Plains such interacting forces might be the following:

(1) *Natural selection for certain genotypes.* This is controlled by the environment that is characteristic of Plains Streams (to what extent this environment may have varied in the past is not fully known, although some inferences have been presented in preceding sections).

(2) *Isolation.* Drainages of the Great Plains have been variously isolated from northern and eastern drainages in Preglacial and Pleistocene time. This isolation would reinforce the selective mechanisms mentioned under (1).

(3) *Mingling of stocks.* This has been due to drainage changes of the Pleistocene alternating with or subsequent to (2) above.

(4) *Direct environmental influence on phenotypic expression.*

Items (1), (2), and (4), above, would, in most instances, tend to yield a more distinctive kind of fish toward the southwest. Item (3) would, in cases where interfertility was unimpaired, tend to produce a more homogeneous population.

The interrelations of isolation and mingling have been discussed by Hubbs (1943:116-117), who states "It will commonly be difficult or impossible to determine whether the intermediate characters of a given population date back to the initial divergence of the two types, or are due to the secondary or subsequent meeting and interbreeding of populations, or of entire forms, which had previously been isolated for some time."

In at least one case—*Hybognathus placitus* and *Hybognathus nuchalis*—the processes of differentiation (just described) between stocks inhabiting a western, Plains Drainage and a more eastern Teays/Mississippi Drainage seem to have progressed far enough to produce different, although closely related, species.

In other instances differentiation has not produced species but has resulted in well-differentiated variants that have been recognized as subspecies (*Notropis s. stramineus* and *missuriensis; Etheostoma s. spectabile* and *pulchellum; Hybopsis aestivalis* sspp.)

In still other instances differentiation may have been less or subsequent mingling may have obscured differences that once were better defined. Such kinds vary over a broad zone of clinal intergradation. Such intergradation is seen to various degrees and in varying patterns between Plains and eastern populations of *Semotilus atromaculatus, Hybopsis aestivalis hyostoma, Notropis atherinoides, Notropis blennius, Pimephales promelas, Campostoma anomalum pullum, Carpiodes cyprinus, Catostomus commersoni* and *Ictalurus melas.*

RECORDS AND COLLECTIONS OF FISHES

An early summary of collections from the Missouri River Basin was compiled by Evermann and Cox (1896). The status of ichthyological collecting in Kansas prior to 1946 was summarized by Breukelman (1946). His account contains many references to the Kansas River Basin. Minckley (1959) listed collections that had been made in the Blue River Basin prior to his work in that stream system.

The earliest reports that are possibly attributable to the Kansas River Basin all seem to deal with catfishes. Thus, Abbott (1861: 568-569) described two new species of "*Pimelodus*" (both probably *Ictalurus punctatus* according to Evermann and Cox, 1896:354) from "Fort Riley, Kansas" and Gill (1862:43, 44; 1876:417-419, Pl. 6) named and discussed *Ictalurus simpsonii* (also identifiable as *I. punctatus*) noting (1862:44) that "Two specimens were obtained by Dr. Suckley in the 'Big Sandy River' of Kansas." The reports of Gill noted above pertain to fishes collected on the expedition of James Hervey Simpson in 1858 and 1859. I find no reference elsewhere in the report of Simpson (1876) confirming the presence of George Suckley on this expedition. According to a chart of magnetic dip (Simpson, 1876:227), some members of the expedition crossed Big Sandy River (also known as Big Sandy Creek or Sandy Creek), a tributary of the Little Blue River in southern Nebraska, on June 12, 1858, and, evidently, again in early October, 1859.

Species named by Abbott (1861:568-569; 1861:473-474), and by Gill (1864:151) and the species reported by Cope (1864, 1865, 1871) were from collections made by Dr. W. A. Hammond. Hammond was a surgeon assigned to an expedition under the command of Lt. F. T. Bryan to explore a route from Fort Riley, Kansas, to Bridgers Pass, Wyoming. The itinerary of the expedition is discussed further in the chapter concerning species of improbable occurrence in the Kansas River Basin.

In 1875 F. H. Snow published a list of the more common fishes found in the Kansas River at Lawrence, Kansas.

In the period 1880-1900 numerous collections were made and recorded in the literature of that time. Serving as a basis for knowledge of fishes of the Basin were the reports of Gilbert (1884, 1885a, 1885b, 1886, 1889) based on material sent him by F. W. Cragin of Washburn University, Topeka, Kansas. A few (mostly types) of the specimens collected by Cragin and his co-workers are still housed at the United States National Museum. However, the part of the collection of Cragin retained at Washburn University was mostly destroyed by fire.

In 1885 Cragin and I. D. Graham (the latter at Kansas State College, Manhattan) issued (separately) the first and, to date, only lists of the fishes known to occur in Kansas. In addition Cragin published a note concerning lampreys (1885a) and Graham (1885b) listed the fishes housed in the museum of Kansas State College (now Kansas State University). Some of the specimens acquired by Graham are still preserved in the holdings of Kansas State University (Breukelman, 1946:54; Jennings, 1942).

As mentioned heretofore, O. P. Hay investigated the fish fauna of northwestern Kansas and reported thereon in 1887. Part of Hay's collections are extant at the United States National Museum.

In 1891 S. E. Meek (1894) collected in the Blue River at Crete, Saline County, Nebraska. Evermann and Cox (1896) reported collections made in 1892 and 1893 in the upper Big Blue River Basin in Nebraska.

The State Biological Survey of Kansas actively collected fishes, many of them from the Kansas River Basin, at various times since 1900 but especially in the years 1910-1912 (Breukelman, 1946:55) and from 1950 to the present. Many of these collections are preserved in the Museum of Natural History, University of Kansas, and the older collections were reported by Breukelman (1940b). Breukelman (1946:55) described the work of Minna E. Jewell, who in the 1920's collected extensively in Kansas. The collection of Jewell is now housed in the Museum of Zoology, University of Michigan. Also housed at that institution are the extensive collections made by Raymond E. Johnson in Nebraska from 1939 to 1941, part of which are from the Kansas River System. Many smaller collections from the Kansas River Basin are also housed at UMMZ, notably those made by W. Ralph Taylor, John Breukelman, Claude Hibbard and C. W. Creaser.

Aside from the collections already mentioned there are a number of smaller collections taken at various times and places from the Kansas River Basin in the holdings of the United States National Museum. Among these are a few specimens taken by F. F. Crevecoeur, who made early observations on the fishes in the Vermillion River near Onaga, Kansas (1903, 1908).

At the Museum of Comparative Zoology, Harvard, a number of specimens are preserved that were taken in the 1800's near Hays and Topeka, Kansas. Some of these collections are credited to "R. Bliss" or "Dr. L. Watson" of Ellis, Kansas (See Evermann and Cox, 1896:360).

At the Academy of Natural Sciences of Philadelphia there are a few old specimens, mostly types, and a number of specimens collected in the Kansas River near Topeka, Kansas, in 1958 in a limnological survey under the supervision of Ruth Patrick.

W. L. Minckley collected in the Big Blue River System of Kansas in 1957 and 1958 and J. E. Deacon and A. L. Metcalf made collections in the Wakarusa River Basin in 1959. Frank B. Cross has made many collections in the Kansas River Basin assisted by various students among whom Bernard C. Nelson should especially be noted. My own collections have been made at various times between 1956 and 1963. The collections mentioned in this paragraph are housed in the Museum of Natural History, University of Kansas.

Species of fishes that have been described from the Kansas River Basin are listed in Table 6. As indicated in the table it is likely that some of the type localities are in error.

For museums from which material from the Kansas River Basin was studied the following abbreviations are used:

ANSP—Academy of Natural Sciences of Philadelphia.
KU—Museum of Natural History, The University of Kansas, Lawrence.
KSU—Kansas State University, Manhattan.
MCZ—Museum of Comparative Zoology, Harvard.
OAM—Oklahoma State University, Stillwater.
UMMZ—University of Michigan, Museum of Zoology.
USNM—United States National Museum.

ACCOUNTS OF SPECIES

Ichthyomyzon castaneus Girard

Four specimens of the "chestnut lamprey" were reported from the mouth of Mill Creek by Cragin (1885a:99). His description of the specimens, specifying that all possessed 3 maxillary (supraoral),

Table 6.—Species for Which the Type Locality Has Been Reported to be in the Kansas River Basin. Species Listed Below the Double Line Are Thought to Have Come From Other Drainages. (*—Big Sandy River May Refer to a Tributary of the Little Blue River in Southern Nebraska. **—According to Jordan and Evermann, 1896.)

Species described	Identification	Type locality	Disposition of types	Remarks
Pimelodus hammondii Abbott	*Ictalurus punctatus*	"Fort Reiley, Kansas"	Not located	W. A. Hammond, Coll.
Pimelodus notatus Abbott	*Ictalurus punctatus*	"Fort Reiley, Kansas"	ANSP 8449	W. A. Hammond, Coll.
Ictalurus simpsonii Gill	*Ictalurus punctatus*	"Big Sandy River, Kansas"*		Type possibly USNM 9718, bearing data "*Ichthaelurus punctatus*, Big Sandy River, Kansas, W. Stimpson"
Catostomus chloropteron Abbott	*Catostomus commersoni*	"Kansas"	Not located	W. A. Hammond, Coll.
Semotilus hammondii Abbott	*Semotilus atromaculatus*	"Kansas"	Not located	W. A. Hammond, Coll.
Percopsis hammondi Gill	*Percopsis omiscomaycus*	"Kansas"	Not located	W. A. Hammond, Coll.
Alburnus oligaspis Cope	*Notropis atherinoides*	"Kansas"	ANSP 2753–54	W. A. Hammond, Coll.
Lepidosteus otarius Cope	*Lepisosteus osseus*	"Platte River near Fort Riley"	Not located	
Notropis topeka Gilbert	*Notropis topeka*	Shunganunga Creek, Topeka, Kansas	USNM 36609	
Minnilus nigripinnis Gilbert	*Notropis umbratilis*	Shunganunga Creek, Topeka, Kansas	USNM 36613	

Notropis aeneolus Hay	*Notropis topeka*	Solomon River at Beloit, Kansas	USNM 37945	
Notropis germanus Hay	*Notropis heterolepis* x *Hybognathus hankinsoni* (Hubbs, 1951)	Smoky Hill River at Wallace, Kansas	USNM 37949	
Etheostoma arcus-celestis Crevecoeur	*Etheostoma spectabile*	Vermillion River System near Onaga, Kansas	Probably none designated	
Fundulus kansae Garman	*Fundulus kansae*	"Big Sandy River, Kansas"*	MCZ 6248	
Rhinichthys maxillosus Cope	*Rhinichthys cataractae*	"Kansas"	ANSP 4984–96	Probably from Platte River System
Gasterosteus micropus Cope	*Culaea inconstans*	"Platte River near Fort Riley"	Not located (Possibly ANSP 14184–85)	Probably from Platte River System
Salmo (Salar) stomias Cope	*Salmo clarki*	"Platte River near Fort Riley"	Not located (Possibly ANSP 7825–26)	Probably from Platte River System
Gila affinis Abbott	*Gila robusta*	"Kansas"	ANSP 4196 USNM 21088**	Probably from Green River System in Wyoming

cusps strongly suggests that the specimens were, in fact, *I. castaneus.* Hubbs and Trautman (1937) listed no further occurrences of chestnut lampreys in the Kansas River System. Bailey (1959b:163) reported *I. unicuspis* Hubbs and Trautman from the Missouri River in South Dakota and suggested that *I. unicuspis* might range farther upstream in the Missouri System than did *I. castaneus.* Cross and Metcalf (1963:187) listed new records of *I. castaneus* from the Missouri River near St. Joseph, Missouri, and in North Dakota and of *I. unicuspis* from Omaha, Nebraska. It seems likely, then, that both species formerly penetrated far up the Missouri River and its main tributaries; as pointed out by Bailey (1959b:163), there may have been a general pattern of extirpation of lampreys in the region in recent years. Cross and Metcalf (1963:187) noted a report by an angler in 1960 of a lamprey from the Kansas River near its mouth. To my knowledge *I. unicuspis* has never been taken from the Kansas River Basin.

Scaphirhynchus platorynchus (Rafinesque)

The shovel-nosed sturgeon is taken frequently in the lower part of the Kansas River and its largest tributaries (Map 1). Westernmost records are from the Republican River, including two early collections and one recent collection as follows: (1) USNM 3246 taken by W. A. Hammond, (2) USNM 3294 taken by Lt. F. T. Bryan on June 23, 1856, and (3) KU 4065 taken by F. B. Cross and Bernard Nelson at Concordia, Cloud County, Kansas, on June 25, 1958. (The earlier records have not been included in Map 1 due to the lack of specific locality data.)

The taxonomic status and some aspects of the ecology of this and the related species *S. albus* have been discussed by Bailey and Cross (1954).

Scaphirhynchus albus (Forbes and Richardson)

The pallid sturgeon has been taken only in the lower Kansas River. It is much less abundant than *S. platorynchus,* which occurs in the same waters. According to Bailey and Cross (1954:201) eight percent of the specimens of *Scaphirhynchus* observed from near Lawrence, Kansas, were *S. albus.* However, since 1952, a year of unusually high water and flooding, no specimens of *albus* have been taken at Lawrence.

Bailey and Cross (1954:174) contended that *S. albus* and *S. platorynchus* are closely related. This being the case the two kinds

probably diverged from an ancestral stock at a time when they were not sympatric as at present. Of the three preglacial drainages mentioned herein (Fig. 3) it seems that the widespread S. *platorynchus* inhabited the Preglacial Teays/Mississippi and possibly the Preglacial Plains Stream and some other southwestern drainages. The most likely area of origin for S. *albus*, on the other hand, seems to be the Preglacial Hudson Bay System, whence it invaded the present Missouri/Mississippi System by deflection southward of north-flowing streams.

Polyodon spathula (Walbaum)

The paddlefish seems restricted to the lower part of the Kansas River proper. Snow (1875:140) wrote "Previous to 1874 only two specimens of this curious fish had ever been taken at Lawrence, but since the building of the dam several have been taken, varying in weight from 1 lb. to 20 lbs., and in length from 2 to 5 feet." The paddlefish still occurs in the vicinity of Lawrence, Kansas (Cross and Hastings, 1956:86) but its rarity is such that a paddlefish snagged by an angler in 1963 received special attention in the local newspaper as an oddity. The westernmost records are from the vicinity of Manhattan, Kansas (Graham, 1885a:70; Jennings, 1942: 364). I have examined one specimen (KSU 4960) taken in 1938 at the mouth of Wildcat Creek, Riley County, Kansas.

Lepisosteus platostomus Rafinesque

The short-nosed gar has been taken only from the Kansas River Mainstream, the lowermost part of some of the largest tributaries, and from oxbow lakes along the Kansas River (Map 2). Further discussion is in the account of *L. osseus*, below.

Lepisosteus osseus Linnaeus

The long-nosed gar is common in the larger, downstream parts of the Kansas River and in some of its major tributaries (Map 3). The long-nosed gar seems to be more common than the short-nosed gar and to ascend smaller tributaries than does the latter. Minckley (1949:415) reported *L. osseus* from 14 stations in the Big Blue River System, *L. platostomus* from only two stations. In the winter of 1956-57, I observed large numbers of dead long-nosed gars and a few short-nosed gars along the Kansas River at Lawrence.

There is some indication that this species once ranged farther

west in the Kansas River Basin than at present. Hay (1887:247) reported it from Beloit on the Solomon River. This record is represented by a juvenile (USNM 37959), 82.5 mm in total length and 17.4 mm in snout-length. An entry (USNM 3244) of February, 1861, in the catalogue of the Division of Fishes, United States National Museum, lists *L. osseus* from the Republican River with Wm. S. Wood as collector. Attempts to locate this specimen were unsuccessful.

Both species of gar reported here, being characteristically species of big rivers, enter the Kansas River Basin along the main channels from the east.

Dorosoma cepedianum (LeSueur)

The gizzard shad is common in the lower part of the Kansas River, in its major tributaries, and in reservoirs in the western part of the Basin (Map 4). It is another of a large number of fishes, typical of big rivers, that ascend the Kansas River from the east.

Salmo trutta Linnaeus and Salmo gairdneri Richardson

The brown trout and the rainbow trout have been stocked in a few streams and springs in the Kansas River System in Nebraska, Colorado, and Kansas. Rainbow trout are placed periodically in Elm Creek, Webster County, Nebraska; Rock Creek, Dundy County, Nebraska, and in several streams in the vicinity of Wray, Yuma County, Colorado. According to members that I have contacted of the Colorado Game and Fish Department and of the Game, Forestation and Parks Commission, State of Nebraska, rainbow trout do not reproduce in these streams. Brown trout have been stocked in some tributaries of the North Fork Republican River in Yuma County, Colorado, and are said to reproduce there. The streams mentioned above are cool, clear brooks deriving their water from the area of Pleistocene sands and gravels or from the base of the Ogallala Formation where it contacts underlying Cretaceous beds.

Hiodon alosoides (Rafinesque)

The goldeye has been taken at numerous localities in the lower Kansas River (Map 5) and in its larger tributaries. Hay (1887: 250) reported it as far upstream as WaKeeney on the Saline River and Concordia on the Republican River (I have checked the identity of the Concordia specimen—USNM 37932). Another specimen

from the Republican River (USNM 3548) bears the data "Republican—Wood." There are reports by fishermen as far west as Scandia, Republic County, Kansas, on the Republican River, and Salina, Kansas, on the Smoky Hill River. Trautman (1957:173, 174) remarked that:

"The Goldeye appears to be far more tolerant of turbid water than is the Mooneye *Hiodon tergisus*. Tolerance to turbidity is indicated by its presence, often in large numbers, in the muddy streams of the Missouri system and those of the province of Manitoba. It is therefore possible that the clear-water inhabiting Mooneye was formerly more numerous in the upper Ohio Drainage than was the Goldeye, but that since the waters of this drainage have become more turbid, the turbid-tolerant Goldeye has become the most numerous."

This tolerance of turbidity and the present distribution of *H. alosoides* both suggest a western or Plains-origin. Perhaps *H. alosoides,* which also possesses northern affinities, originally inhabited the Preglacial, north-flowing Missouri River and became a part of the fauna of the Ancestral Plains Stream after deflection of the Ancestral Missouri southward into the Ancestral Plains Stream Drainage at the onset of glaciation. Subsequently, it has extended its range eastward. *Hiodon tergisus,* on the other hand, may have evolved in the Preglacial Teays/Mississippi System.

Esox lucius Linnaeus

Although occurring farther north in the Missouri River Basin (Evermann and Cox, 1896:415; Bailey and Allum, 1962:33), the northern pike does not seem to have been native to the Kansas River System. Both Cragin (1885b:110) and Graham (1885a:78) noted that the northern pike had been introduced in Kansas. Lack of subsequent records indicates, however, that these early introductions were unsuccessful. More recently northern pike have been planted in several reservoirs of Nebraska (I observed a large specimen taken in Harlan County Reservoir), Kansas (Tuttle Creek and Webster reservoirs, R. E. Schoonover, personal communication) and in Bonny Reservoir in Yuma County, Colorado (McCarraher, 1961:228).

Cyprinus carpio Linnaeus

Graham (1885a:78) and Cragin (1885b:109) listed carp as having been planted in Kansas, and Dyche (1914:125) noted that it was found in nearly all Kansas streams. At present it occurs throughout the Basin. It is less abundant in the smaller, clearer

tributaries having high gradient than in rivers, but it is not completely alien to small streams. In the headwaters of Medicine Creek at Wellfleet, Nebraska, one of the most turbid creeks in the Kansas River Basin (Secchi disc approximately six inches), carp approximately one foot long were observed in a brook eight to 15 feet wide and rarely as deep as three feet.

Carassius auratus (Linnaeus)

The goldfish has been reported from a few, scattered localities in the Kansas River Basin; it does not seem to have become common.

Notemigonus crysoleucas (Mitchill)

The golden shiner has been taken in the extreme eastern and extreme western sections of the Kansas River Basin (Map 6) but there are no records from the central part. Minckley (1959) failed to take the golden shiner in his extensive survey of the Blue River Basin in Kansas. Several of the western records are in or near impoundments. That *N. crysoleucas* may not be native to these western waters is given credence by Breukelman (1940:370): "The only specimens on record are two series we obtained on the 1938 field trip; one from Beaver creek below the Lake Atwood dam and the other from the Saline river below the Sheridan county dam. At both places fishermen reported the species common. Since this is an easily recognized fish it was probably not present in any considerable numbers until recently; the earlier collectors would not all have missed it."

There are no verifiable records of *N. crysoleucas* from the Kansas River Basin prior to the 1930's, although Graham (1885a:74) listed it from "Eastern Kansas." Probably this cyprinid is native to the extreme eastern part of the basin but it has not penetrated far westward.

Most records from the extreme eastern section of the basin are from creeks. Deacon and Metcalf (1961:316), in a survey of the Wakarusa River System, reported the species from 5 stations—all on tributaries of the Wakarusa River Mainstream.

Semotilus atromaculatus (Mitchill)

Habitat and Distribution.—The creek chub is common in the Kansas River Basin except in the drainage of the upper Big Blue River (Map 7), an area of especially silty streams with muddy

TABLE 7.—RANGES AND MEANS OF LATERAL-LINE SCALES FOR SOME SPECIMENS OF *Semotilus atromaculatus*. ARRANGEMENT OF LOCALITIES IS NORTH TO SOUTH BY STREAM SYSTEM AND EAST TO WEST WITHIN EACH STREAM SYSTEM.

Locality	Range	Mean	No.
Niobrara River Drainage:			
Nebraska, Antelope County, Verdigre Creek (KU 7170 and KU 7227)	55–63	59.5	10
Platte River Drainage:			
Nebraska, Dixon County, Logan Creek (KU 7156)	52–63	58.3	16
Nebraska, Keith County, North Platte River at Keystone (KU 4851)	57–65	60.4	10
Colorado, Douglas County, Tributary of Cherry Creek (KU 5518)	55–67	60.6	25
Colorado, Larimer County, Big Thompson River (KU 4774)	57–62	58.9	10
Colorado, Larimer County, Tributary of Cache la Poudre River at Livermore (9 September 1959) (KU 4804)	56–67	62.2	10
(2 September 1960) (KU 5530)	56–65	60.1	15
Wyoming, Albany County, Laramie River, 17 miles north Laramie (KU 4812)	55–63	59.1	20
Lower Missouri River Drainage:			
Missouri, Moniteau County, Moniteau Creek (KU 6490)	55–64	59.7	16
Missouri, Morgan County, Richland Creek (KU 6458)	56–65	60.0	12
Kansas River Drainage:			
Kansas, Douglas County, Tributary of Kansas River (KU 1290)	54–61	57.6	11
Kansas, Shawnee County, Shunganunga Creek (KU 1954)	56–65	60.0	10
Kansas, Riley County, Deep Creek (14 December 1957) (KU 3869)	54–65	59.4	14
(7 September 1961) (KU 7219)	56–67	60.6	18
Nebraska, Webster County, Elm Creek (Republican River Drainage) (KU 7052)	55–67	61.0	16
Kansas, Scott County, Timber Creek (KU 4012)	53–63	57.3	9
Kansas, Wallace County, Rose Creek (Smoky Hill River Drainage) (KU 4023 and KU 7207)	54–63	58.7	14

Table 7.—*Concluded.*

Locality	Range	Mean	No.
Nebraska, Hitchcock County, Frenchman Creek at Enders Dam (KU 4855)	56–65	59.5	20
Arkansas River Drainage:			
Missouri, Ripley County, Tributary of Eleven Point River (KU 6583)	55–61	58.1	10
Arkansas, Franklin County, Spirit Creek (KU 6293)	53–60	56.1	15
Arkansas, Benton County, McKisic Creek (Elk River Drainage) (KU 4557)	54–61	57.6	14
Oklahoma, Mayes County, Tributary of Neosho River (KU 6899)	56–60	58.0	10
Kansas, Upper Neosho Drainage (Composite)	57–63	58.7	7
New Mexico, Colfax County, Cimarron River at Springer (KU 4218)	52–58	55.0	10
New Mexico, Mora County, Mora River at Valmora (KU 4234)	51–59	53.8	18
Red River Drainage:			
Arkansas, Montgomery County, Caddo River (KU 6159)	51–55	52.7	10
Arkansas, Sevier County, Winters Creek (KU 6108)	51–58	53.6	10
Trinity River Drainage:			
Texas, Nacogdoches County (Composite)	51–55	52.4	7

bottoms. As suggested by its common name, this species prefers small, upland streams. Only two records are known to me from the lower 100 miles of the Kansas River Mainstream, although the species abounds in creeks on both sides of the mainstream.

Variation.—A check of some meristic characters and body-proportions of specimens from several localities revealed only slight variation. West of the Mississippi, scale-size seems to increase from north to south. A similar southward increase in scale-size was noted in eastern populations by Bailey, Winn and Smith (1954:124). Some counts of lateral-line scale are in Table 7. Ventral scales tend to decrease in size and to become embedded in a thick epidermis in some western tributaries of the upper Platte and Kansas river systems.

Eye-size diminishes westward, as in several other species of wide occurrence in the Great Plains (Table 8). In western streams of the Platte and Kansas systems the skin surrounding the eye thickens and extends inward slightly, sheathing the peripheral surface of the eye. Two mechanisms seem at work here to decrease the amount of eye-tissue exposed to the environment, suggesting that this reduction has adaptive value to western representatives of this species.

Populations from the Kansas, Arkansas, and Red River systems differ subtly from those of the Platte River in possessing (1) deeper bodies, slightly thicker anteriorly, (2) longer and deeper heads and (3) a more decurved anterior dorsal profile. Populations from the upper Canadian and Pecos rivers in northeastern New Mexico are exceptional in possessing a smaller head.

Zoogeography.—This species has been reported as a mid-Pleistocene fossil from southwestern Kansas and northwestern Oklahoma (C. L. Smith, 1958:178; G. R. Smith, 1963:279), and it now occurs as a relict in the upper Canadian and Pecos river systems. Probably it occurred in the drainage of the Ancestral Plains Stream. How-

Table 8.—Corneal Width (Expressed in Thousandths of Standard Length) of Some Specimens of *Semotilus atromaculatus* (40-50 mm in Standard Length). Localities Are Arranged Generally in an East-West Manner.

Locality	Range	Mean	No.
Kentucky, Bullitt County, Rolling Fork River Drainage (KU 4105 and 5707)	69–76	73.1	10
Wisconsin, Iowa County, Tributary to Trout Creek (KU 5381)	73–85	76.5	26
Arkansas, Montgomery County, Caddo River (Ouachita River Drainage) (KU 6915)	71–81	74.8	10
Missouri, Morgan County, Richland Creek (Missouri River Drainage) (KU 6458)	67–78	72.9	7
Kansas, Shawnee County, Shunganunga Creek (Kansas River Drainage) (KU 1954)	64–71	67.5	10
Nebraska, Webster County, Elm Creek (Republican River Drainage) (KU 7052)	62–71	65.6	12
Wyoming, Albany County, Laramie River (North Platte River Drainage) (KU 4812)	60–67	63.2	12
New Mexico, Colfax County, Cimarron River at Springer (KU 4218)	60–70	62.9	14

ever, diversion of the Kansas River eastward placed any populations previously inhabiting that basin in contact with populations to the east, in the Mississippi Valley. Presently, populations in the Kansas River resemble those to the east, and characters that do vary show smoothly clinal change from east to west or northeast to southwest. The differences that I found in western creek chubs (smaller eye, smaller scales and a chubbier body) seem too slight to merit taxonomic recognition.

Chrosomus erythrogaster (Rafinesque)

Habitat and Distribution.—At present the southern red-bellied dace is found in the Kansas River Basin (Map 8) only in streams of the Flint Hills Area, where it is restricted to headwaters of creeks, usually near springs. Within the limited confines of this habitat it is often abundant.

Evidence of a former, more widespread distribution is provided by the record of Hay (1887:249) from Lenora, Norton County, Kansas. I have examined a specimen (USNM 38241), collected by Hay at this locality, that has the small scales and looped intestine characteristic of *C. erythrogaster* and possesses 8 anal rays. Although suffering much depigmentation, there are still discernible two dark lateral bands as in *Chrosomus eos* Cope and *C. erythrogaster.* A few scattered melanophores dorsal to the upper band suggest the presence, originally, of spots in that region. The mouth is long and subhorizontal as in *C. erythrogaster,* not short and strongly oblique as in *C. eos.*

Chrosomus erythrogaster seems to be one of a number of species that has suffered restriction of range in the Kansas River Basin since settlement of the land and subsequent modification of the watershed.

Zoogeography.—To my knowledge the southern red-bellied dace does not occur north of the Kansas River Basin in the Missouri River System. In the Platte and Niobrara drainages both *C. eos* Cope and *C. neogaeus* (Cope) are found. To the south in parts of the Arkansas River and Red River drainages, *C. erythrogaster* prevails. *C. erythrogaster* is also common in the Ozark Region, including Ozarkian tributaries of the lower Missouri River. It seems probable, then, that *C. erythrogaster* entered the Kansas

River Basin from the Ozark Region. Probably it has occupied the eastern part of the Basin for a long period of time, as streams east of the Flint Hills have long flowed eastward toward the Ozark Region.

Hybopsis gracilis (Richardson)

Habitat and Distribution.—The flat-headed chub has been taken only rarely in the Kansas River Basin. All collections are from streams with sandy bottoms. Olund and Cross (1961:334-336) discussed the habitat of the species in the Great Plains. *H. gracilis* has an unexplained disjunction in its distribution in the Kansas River Basin, having been taken in the lowermost part of the mainstream and again, after a hiatus of approximately 200 miles, in the upper Republican River (Map 9). There are no records to suggest a former, more widespread distribution.

Zoogeography.—Olund and Cross (1961) recognized two subspecies of *Hybopsis gracilis.* They mapped the typical subspecies (Pl. 21) as occurring in the Mississippi River, below the mouth of the Missouri River, in the Missouri River and some of its northwestern tributaries and in the basins of the Mackenzie and Saskatchewan rivers of Canada. The other subspecies, *H. g. gulonella,* was found to occur in some western tributaries of the Missouri River and in the upper Arkansas, Pecos and Rio Grande drainages. Many populations from the Missouri River Basin, including those from the Kansas River Basin, were considered intergrades between the two subspecies.

Bailey and Allum (1962:44) suggested that differences in water temperature between the Missouri River and its western tributaries produce, through phenotypic modification, the morphological differences that were observed by Olund and Cross and thought by the latter authors to deserve taxonomic recognition. Bailey and Allum (1962:44) noted that the upper Missouri River is fed by mountain tributaries and remains relatively cool throughout the summer. It should be pointed out, however, that the North Platte River, in which *H. g. gulonella* occurs, is also fed by tributaries carrying melt-waters from mountains in northern Colorado and southern Wyoming. Olund and Cross (1961:333) found populations of *H. g. gulonella* at the uppermost stations sampled on the

North Platte River where summer temperatures of water presumably are colder, whereas downstream where waters become warmer there was evidence of intergradation with *H. g. gracilis*. This suggests a zone of intergradation of different kinds of fishes rather than a purely phenotypic response. The upper Arkansas River is also fed by mountain streams carrying meltwaters throughout the summer from the massive Sawatch Range and other mountain ranges of Central Colorado. Specimens collected from the upper Arkansas River also have the phenotype of *H. g. gulonella*. Flathead Chubs were taken at Florence, Fremont County, Colorado, on September 7, 1959, in water at 65° F. It can be argued, of course, that it is not known whether these fish undergo their early development in these waters. However, the upper Arkansas River has few tributaries and most of these also drain mountainous areas.

The present distribution of *H. g. gulonella* suggests that it differentiated in the Ancestral Plains Stream. If so, a question remains concerning when and where *H. g. gracilis* was sufficiently separated from the stock of incipient *H. g. gulonella* to diverge racially from it. Possibly *H. g. gracilis* inhabited the Preglacial Missouri River described by Meneley, Christiansen and Kupsch (1957). This stream possessed, as headwaters, the present-day upper tributaries of the Missouri River but flowed northeastward into Hudson Bay. Perhaps with the advent of glaciation and diversion of the upper Missouri southward into the Ancestral Plains Stream, populations of *H. g. gracilis* commingled with *H. g. gulonella*, the latter kind having held forth in that segment of the Ancestral Plains Stream south of the divide between Hudson Bay and the Gulf of Mexico that lay somewhere in the vicinity of present-day South Dakota (Flint, 1955:148). Such a northern origin might account for the preference of *H. g. gracilis* for the cooler waters of the Missouri River over the adjacent downstream parts of its western tributaries and for its reinvasion of the Saskatchewan and Mackenzie drainages of Canada since the last glaciation there. The hypothesis of an origin in the ancestral north-flowing Missouri System might explain the absence of *H. g. gracilis* from the upper Mississippi and Ohio rivers and in the Red River of the North. A cold-tolerant fish inhabiting an eastern relicitium in the central Mississippi Valley would be expected to have ascended the Mississippi and to have entered the Red River through the well-documented connection to Lake Agassiz offered by the River Warren (Underhill, 1957:7).

Hybopsis biguttata (Kirtland)

Habitat and Distribution.—At present the horny-headed chub seems to have one of the most restricted ranges of any fish found in the Kansas River Basin (Map 10). It has, in recent years, been taken only in Mill Creek, Wabaunsee County, Kansas (KU 2968). There are a number of earlier records that indicate that the species was formerly much more widespread in the Basin. Specimens that I have examined are listed in Table 9.

In discussing the status of this species in northwestern Kansas, Breukelman (1940:370) noted that, "Careful seining of Hay's localities at the same time of the year in 1938 failed to reveal a single specimen. Questioning of fishermen indicated that if present in northwestern Kansas, the species is very rare. In view of the fact that large specimens of this clearwater species are not apt to be misidentified, a change in the fauna of the area seems to have occurred." In the case of Rock Creek, Douglas County, the species seems to have disappeared since 1941 (Table 9) as frequent collections made since 1950 have failed to reveal it there.

Elsewhere in the Missouri River System *H. biguttata* is known at present only from a few rather widely separated areas: (1) the Ozark Region of Missouri, (2) a few creeks in eastern Wyoming

Table 9.—Early Records of *Hybopsis biguttata* (Kirtland) From the Kansas River Basin.

Museum number	Locality	Date collected
USNM 3552	"Republican"	probably 1857
MCZ 18480	Fort Hays, Kansas	1871
MCZ 18483	Fort Hays, Kansas	1871
UMMZ 86429	Fort Hays, Kansas	1871
KU 8188	Saline River, Trego County, Kansas	
KU 403, 416, 420, 423-429, 587, 593	Rock Creek, Douglas County Kansas	1898
KU 389, 391, 392	Rock Creek, Douglas County, Kansas	1899
UMMZ 63170	Rock Creek, Douglas County, Kansas	1924

(Simon, 1946:71 and KU 4813), and (3) the area drained by the Big Sioux and Floyd rivers in Iowa (Cleary, 1956:Map 37). Older records (Hay, 1887:250, 252; Evermann and Cox, 1896:410; Ellis, 1914:62) indicate that the species was more widespread in the Missouri River Basin in the past.

Disjunctions in range that now exist, with preservation of only a few semi-relict populations in especially favorable streams, suggest a process of extirpation over much of the Missouri River Basin. A similiar pattern was observed by Trautman (1957:294), who traced the decrease in abundance of the horny-headed chub in several Ohio streams.

Greene (1935:75) described the preferred habitat of the horny-headed chub as ". . . clear water, moderate current with some gravelly riffles and a moderate amount of aquatic vegetation." Some or all of the requisites specified by Greene are thought to have disappeared from much of the basin of the Kansas River during the years since settlement began. Water in streams has, in many parts of the basin, decreased in clarity and in constancy and volume of flow. Decrease in constancy of flow may have been deleterious to growth of aquatic plants. Siltation due to cultivation may have increased fine sediment on stream-bottoms at the expense of coarser sediments, especially in the central part of the basin. Greene (1935:76) and Lachner (1952:435) pointed out the need of *H. biguttata* for gravelly areas at the time of spawning; gravel is needed to build the "nest" characteristic of the species.

Zoogeography.—As pointed out by Bailey and Allum (1962:121), *H. biguttata* is not a typical inhabitant of large, turbid streams. Probably it made its way up the Missouri River System from the Ozark Region at times when conditions were less inimical, or by a process of "tributary-hopping." One now sees this process somewhat in reverse, with extirpation from all but a few of the tributaries in which the species had established populations prior to settlement.

Hybopsis storeriana (Kirtland)

The silver chub is taken frequently in the lower mainstream of the Kansas River but is rare upstream (Map 11). The westernmost record is UMMZ 134348—Republican River, 1¼ miles east of Benkelman, Dundy County, Nebraska, July 24, 1939 (one specimen). Other marginal records to the west include (1) KU 439—Repub-

lican River, Clay Co., Kansas, 1910, (2) KU 8129—Kansas River at Junction City, Geary Co., Kansas, May 9, 1964, (3) UMMZ 122191 —Wildcat Creek, Riley Co., Kansas, September 7, 1923 and (4) KU 3810—Blue River, 1 mile south of Rocky Ford Dam, Riley Co., Kansas, April 6, 1957. Hay (1887:250) reported, with some reservation, *H. storeriana* from WaKeeney, Trego County, Kansas. Breukelman (1940:370) questioned the validity of this identification. I was unable to find specimens of *H. storeriana* among Hay's collections from WaKeeney at the U. S. National Museum. There are, however, 3 specimens (USNM 37938) referable to this species bearing the locality data "Wallace, Kansas." Hay (1887:250) mentioned that the specimens from WaKeeney had lost their scales and were otherwise in poor condition. This characterization applies to USNM 37938 and it seems possible that the locality data are in error. (I have not included *H. storeriana* in Table 5, which lists species taken by Hay at Wallace.) Perhaps the failure to take *H. storeriana* frequently in upper tributaries of the Kansas River System in recent years is related to a decreased volume of flow in those streams. In this respect *H. storeriana* is like *Hiodon alosoides* and *Lepisosteus osseus*. Several writers have pointed out the proclivity of the silver chub for large streams. Forbes and Richardson (1909:167) noted that it was a fish of larger streams and lowland lakes. Greene (1935:79) characterized it as typical of "large-water fishes of southern range." Greene's comment seems pertinent to this species in the Kansas River Basin as it seems to have penetrated from the east along the larger streams.

Hybopsis meeki Jordan and Evermann

Habitat and Distribution.—The sickle-finned chub has been taken only in the lower mainstream of the Kansas River and seems rare there (Map 12). Three records, consisting of one specimen each, are known to me: KU 1842 and KU 2172 taken on October 24, 1951, and April 5, 1952, respectively, below the dam at Lawrence, Douglas County, Kansas, and one specimen taken on April 20, 1962, at Eudora, Douglas County, Kansas, but not preserved.

Zoogeography.—Bailey and Allum (1962:48, Fig. 5) have mapped known records of the sickle-finned chub and pointed out its virtual restriction to the Missouri River and that part of the Mississippi River downstream from the mouth of the Missouri.

Such a distribution suggests an origin in the ancestral, north-flowing Missouri River. Possibly a stock ancestral to this species and to *Hybopsis storeriana* gave rise to the former in the ancestral, north-flowing Missouri and to the latter in the Teays/Mississippi System in pre-Pleistocene time. From the upper Mississippi *H. storeriana* penetrated northward soon enough after the last glacial retreat to enter the Red River (Underhill, 1957:29); whereas, in the upper Missouri River it has penetrated only as far northward as southeastern South Dakota according to Bailey and Allum (1962:46).

Hybopsis aestivalis hyostoma (Gilbert)

Habitat and Distribution.—Most records of the speckled chub are from the sandy mainstream of the Kansas, Big Blue, and Republican rivers (Map 13). Available records suggest that it ascends far upstream in the Republican River but not in the Smoky Hill River. The same is true of *Hybopsis gelida* and *Hybopsis gracilis.* The reason for this is not clear.

In the summer of 1961, *H. a. hyostoma* was abundant in the Kansas River below Bowersock Dam at Lawrence, Douglas County. Abundant populations are also indicated by a collection of 122 specimens (UMMZ 135100) by R. E. Johnson on July 17, 1940, in the Republican River, one mile south of Indianola, Red Willow County, Nebraska. This collection contained females distended with eggs as did another collection taken on the following day in Blackwood Creek, Hitchcock County, Nebraska.

Variation and Zoogeography.—As pointed out by Greene (1935: 79) *H. aestivalis* seems to have southern affinities, judging from its occurrence in Gulf Coast drainages from the Rio Grande to the Choctawhatchee River in Florida (Yerger and Suttkus, 1962:327). Northward, the species is a hesitant invader. Bailey and Allum noted (1962:108) that the northernmost record in the upper Mississippi Drainage is in Vernon County, Wisconsin. (Another peripheral record in this area is USNM 118910 taken by Surber at Brownsville, Houston County, Minnesota in 1928.) Bailey and Allum (1962:108) further stated that there are no records of *H. aestivalis* above the Platte River Drainage in the Missouri River Basin. In these preferences *H. aestivalis* exhibits a tendency opposite to that of *H. gracilis* and *H. gelida,* which flourish northward and at higher elevations.

Hybopsis aestivalis, as now recognized, comprises two diverse kinds as regards number of barbels. One, a widespread, two-barbeled kind, is found in much of the Mississippi River System and in some Gulf Coast drainages. The other, a four-barbeled kind, is found in the Arkansas and Red rivers in the west and in the Escambia and Choctawhatchee rivers in the southeast (Yerger and Suttkus, 1962:327). To my knowledge there has been no adequate demonstration of intergradation between these kinds. The problem of relationship of the populations of *H. aestivalis* occupying the various streams of the Gulf Coast and southwestern tributaries of the Mississippi River is complex and in need of study.

Within the range of the widespread two-barbeled chub (to which populations from the Kansas River System appertain) there is variation from east to west; smaller eyes, smaller scales, a more naked venter, longer barbels, and smaller melanophores characterize western populations. Some writers have considered this variation deserving of taxonomic recognition. Breukelman (1940:380) employed the name "*Extrarius aestivalis: sesquialis x tetranemus*" for speckled chubs from the Kansas River System. Breukelman seems to have appreciated the fact that in the characters mentioned above, which distinguish Missouri River populations from those of the Ohio River, that the former parallel to a slight extent those found in the Arkansas and Red rivers. Notwithstanding this parallelism, the difference in number of barbels, a much smaller eye and a more extreme decurvature of the snout readily distinguish populations in the Arkansas and Red rivers from Missouri River representatives.

As this fish inhabits the larger rivers of the Mississippi Valley, gene-flow must be considerable between populations. Some specimens that I have observed from the Mississippi River seem intermediate between those found in the Ohio and Missouri Rivers whereas other specimens closely resemble one or the other. The Mississippi River probably acts as a "mixing bowl" for this and other large river species, receiving gene flow from its major tributaries, mixing these strains and probably providing gene flow back towards tributaries as well, thereby slowing any tendency toward speciation. As the zone of intergradation between extremes of the two-barbeled fraction of *H. aestivalis* in the Mississippi River System is wide and ill-defined it seems best to consider it one taxon in accordance with

the principles suggested by Bailey, Winn and Smith (1954:148-149). In this case, however, retention of a trinomial is necessary at least until such time as the status of the four-barbeled kinds and other named subspecies of the Southwest is elucidated. As *Hybopsis aestivalis hyostoma* (Gilbert) is the oldest available name for the two-barbeled form of the Mississippi Basin, it is here employed to include populations of the Kansas River.

As mentioned above, Breukelman (1940:380) employed the name "*sesquialis*" in referring to Kansas River populations of this species. However, "*sesquialis*" is a *nomen nudum*. An earlier and seemingly available name, applicable to populations of the upper Missouri Basin, is *Hybopsis montanus* Meek. Although this name was placed in the synonymy of *Notropis stramineus* by Bailey and Allum (1962:68), Meek's description (1884:526) of a barbeled minnow seems to apply to *H. aestivalis* and he allied *H. montana* with *H. aestivalis* in this description. Three specimens among the types in the national collection, labeled *H. montanus* and bearing the number indicated by Meek in the original description (USNM 36882), are *H. aestivalis*. There are two labels in the jar, bearing the inscriptions (1) "Hybopsis montanus, E. Slope Rocky Mts., F. V. Hayden" and (2) "Hybopsis montanus, Jordan and Meek (Type) Upper Missouri Region. Dr. F. V. Hayden." In number of barbels, eye-size, scalation, head-shape, and body proportions, these specimens are like *H. aestivalis* from the Missouri River Basin.

Hybopsis gelida (Girard)

Records of the sturgeon chub in the Kansas River System were listed by Cross (1953:90) and Bailey and Allum (1962:46, 47). The species has been taken on numerous other occasions in the Kansas River near Lawrence and Eudora, Kansas (Map 14). Two recent additional records are: (1) KU 8111—Kansas River at Willard, Shawnee Co., Kansas, May 9, 1964 (1 specimen) and (2) KU 8124—Smoky Hill River at U. S. Highway 77, south of Junction City, Geary Co., Kansas, May 9, 1964 (3 specimens). These last-enumerated collections bridge, to some extent, a hiatus that previously existed between downstream records in eastern Kansas and records in the upper Republican River in southwestern Nebraska.

Cross (1959:90) noted that *H. gelida* was locally abundant in the Kansas River near Lawrence, 42 specimens having been secured there between October, 1951, and June, 1952 (years of heavy rain-

fall). UMMZ 135099 also consists of a large series (54 specimens) taken in the Republican River, one mile south of Indianola, by R. E. Johnson on July 17, 1940. The present distribution of *H. gelida* almost exclusively in the Missouri River System suggests that it may have evolved in the Preglacial north-flowing Missouri System. Possibly the same ancestral stock gave rise in the Teays/Mississippi and Preglacial Plains System to *H. aestivalis.*

Phenacobius mirabilis (Girard)

Distribution and Habitat.—The sucker-mouthed minnow occurs widely in the Kansas River Basin and in habitats ranging from the Kansas River Mainstream to small, upland tributaries (Map 15). The largest concentrations were found in tributaries of the Wakarusa and Delaware rivers in the eastern part of the basin.

Zoogeography.—Knowledge concerning the present and past distribution of *P. mirabilis* suggests that it evolved in the Ancestral Plains Stream. The species is widely distributed and common in the streams that probably comprised this drainage.

Minckley and Craddock (1962:374) suggested a possible western origin for this species, stating, "Of the five species of *Phenacobius,* one, *P. mirabilis,* may have arisen from stock isolated west of the St. Louis Embayment and/or the line of Pleistocene glaciation (possibly in the Ozarkian Region). This form became adapted for life in the sandy, variable streams of the Plains . . ." The Ancestral Plains Stream probably was the western drainage involved.

P. mirabilis has invaded some waters peripheral to the drainages that were, in part, contained in the Ancestral Plains Stream, but its penetration has been slight in some directions and probably of a recent nature in others.

Presumably, after western drainages were diverted into the middle reaches of the Mississippi System, this fish followed the Missouri River downstream. In the Mississippi River it penetrated northward to southwestern Wisconsin where Greene (1935:115) characterized it as a fish of southern origin, and to southeastern Minnesota (Underhill, 1957:15). Eastward from the Mississippi its spread seems to have occurred partly in recent time and to have been rapid. Forbes and Richardson (1909:159) noted, "This little fish is, in Illinois, upon the eastern border of its range." Trautman (1957:323) stated, "Before 1800 this plains-inhabiting species presumably ranged only as far eastward as the Mississippi River, except perhaps for outlying and/or existing relict, eastern populations."

Trautman traced the invasion of this species eastward into and across parts of Ohio, correlating the extension of range with the spread of land-use practices that resulted in an increase in turbid, prairie-type streams with silty bottoms. Zahuranec (1962:843) recorded an additional eastward penetration of this species in Ohio, which he also correlated with increased siltation of streams.

Northward from the Platte River in the Missouri River Basin, *P. mirabilis* has not penetrated far. According to Bailey and Allum (1962:54), it has not been reported north of the Platte River in Nebraska and only once in South Dakota. However, Cleary (1956, Map 40) reported it from several tributaries of the Missouri River in northeastern Iowa.

Southward in the Great Plains Region *P. mirabilis* is found in the Red River System (Lewis and Dalquest, 1957:42; Riggs and Bonn, 1959:162), and rarely in some coastal drainages of Texas according to Hubbs and Herzog (1955:69-71). Probably, part of the Ancestral Red River was incorporated in the Ancestral Plains Stream, and possibly one or more of the coastal streams of Texas had connections to this system. The evidence of Quinn (1957:160) for widespread alluviation in Sangamonian time in the lower parts of Texas coastal streams such as the Brazos and Colorado and eventual transgression of interstream divides might, in addition to extensive flooding (Hubbs and Herzog, 1955:70), have led to major interchanges of faunas in streams of this region. Such interchange may account for the infrequency, noted by Clark Hubbs (1957: 102), with which species-ranges correlate with present stream-systems in Texas.

Notropis atherinoides Rafinesque

Habitat and Distribution.—In the Kansas River Basin the emerald shiner is clearly a species of the larger rivers. All collections in the Basin are from the mainstream of the Kansas and Republican rivers or from the lowermost parts of the largest tributaries of these streams (Map 16). Although seemingly tolerant of turbid streams with sandy bottoms *N. atherinoides* does not penetrate far west in the Basin, even though sandy streams are common westward.

Variation.—Recently Bailey and Allum (1962:57) placed *Notropis percobromus* (Cope) in the synonymy of *N. atherinoides.* Previously, *N. percobromus* had been considered (Hubbs, 1945:

16-17) a related but distinct species inhabiting the Great Plains. Bailey and Allum (1962:57) found that "Plains collections average somewhat chubbier in body form, as measured by head depth, body depth, or peduncle depth, and the head is usually a bit longer . . . But these and other characters vary with locality and are not geographically consistent." Variability in body proportions was observed also in series examined from the Kansas River Basin. For example, means of body depth (taken at dorsal insertion) divided by standard length varied from 205 to 229 for collections that I examined from the Kansas River Basin. Three collections made in the Kansas River in Douglas County, Kansas, yielded means as follows: 205 (November, 1957); 207 (October, 1951); and 212 (April, 1961). This same proportion also showed much variation in three series of ten specimens each from the Arkansas River Basin: 201 (September, 1951, North Canadian River, Beaver County, Oklahoma); 214 (April, 1953, Spring River, Cherokee County, Kansas); and 225 (June, 1958, Medicine River, Barber County, Kansas). Despite this variability, which is probably due in part to seasonal nutritional or reproductive fluctuations, populations in the Great Plains usually have mean values greater than 200; populations east of the Mississippi yield mean values less than 200 for the same character. Measurements of distance across the exposed part of the eye revealed less variability than in the case of body depth. Western populations seem consistently to have a smaller exposed surface. However, this smallness is achieved differently in populations in the Kansas River System than in those in the western part of the Arkansas River System. In the latter the cornea is actually small, but in the former the cornea is larger, approaching the size found in eastern populations. The periphery of the cornea is covered by an ingrowth of thin skin. Although different mechanisms are at work, approximately the same area of the cornea is exposed in both cases. Distance across the exposed surface of the eye divided by standard length yielded means of 74 to 77 for six lots from the Kansas River System and 73-75 for three lots from the Arkansas River System in Kansas and western Oklahoma.

Zoogeography.—Possibly a member of the *Notropis atherinoides* complex occupied the Ancestral Plains Drainage. This seems likely since related kinds are found in the Brazos and Rio Grande (Bailey and Allum, 1962:60), suggesting an early penetration southwestward

by members of the group. Also the weak clinal differences seen in Plains populations may be a heritage from a slightly differentiated stock of the Ancestral Plains Drainage and not due entirely to ontogenetic responses to environmental stimuli as suggested by Bailey and Allum (1962:60).

Notropis rubellus (Agassiz)

Habitat and Distribution.—In the Kansas River Basin the rosy-faced shiner seems to be almost confined to Mill Creek in Wabaunsee County, Kansas, where it is common (Map 17). This is a clear, upland stream having rubbly bottoms and frequent riffles. Such a restricted range might provide grounds for suspecting transfer of this species through Lake Wabaunsee on the headwaters of Mill Creek from the Neosho or Marais des Cygnes rivers to the south. However, Gilbert (1886:208) reported "*Notropis rubrifrons*" from a tributary of Mill Creek and from Blacksmith Creek immediately east of Mill Creek many years before construction of Lake Wabaunsee. Gilbert specified that "The males were flushed with brick-red on head and bases of fins." This coloration together with the fact that the specimens came from small, upland creeks make it probable that Gilbert's specimens were actually *N. rubellus* and not the related species of larger streams, *N. atherinoides.* The only other record of *N. rubellus* from the Kansas River Basin is that of Minckley (1959:420) based on one specimen (KU 4195) taken in a small tributary of the Big Blue River.

Proportional measurements made on specimens from Mill Creek, from the Neosho River System and from the Missouri River System (Osage River in Kansas and Richland Creek, Morgan County, Missouri) suggested that affinities of the specimens from Mill Creek were with those from tributaries of Missouri River (Table 10). These populations had deeper bodies and a larger head and eye than did specimens from the Neosho River.

Zoogeography.—*Notropis rubellus* is unknown in the Missouri River Basin north of the Kansas River (Bailey and Allum, 1962:60) and, therefore, probably did not disperse downstream from the north. Ingress to the System was probably from the northern Ozarks to the east. The species may long have inhabited the eastern part of the Basin as this part has consistently drained eastward into the Mississippi System. The population in Mill Creek seems semi-relict; possibly the species is on its way to extirpation in the Basin.

Table 10.—Some Body Proportions (Expressed as Thousandths of Standard Length) of *Notropis rubellus* (35-45 mm Standard Length) (D. O. to L. L. = Distance From Origin of Dorsal Fin Perpendicularly to Lateral Line; S. L. = Standard Length).

Locality and Number of Specimens Examined	Head length/Standard length			D. O. to L. L./Standard length		
	Range	Mean	S. D.	Range	Mean	S. D.
Missouri, Morgan County, Richland Creek (20) (KU 6449)....	263–286	275	5.9	129–142	133	3.0
Kansas, Composite from Osage River (22).....	269–301	280	8.4	125–148	138	7.0
Kansas, Wabaunsee County, Mill Creek (32)..... (KU 2952, 2967, and 3759)	270–303	286	9.9	130–149	140	5.5
Kansas, Composite from Neosho River (33).....	242–287	268	11.7	117–134	125	5.8

Notropis umbratilis (Girard)

Distribution and Habitat.—All collections of the red-finned shiner are from the eastern part of the Kansas River Basin, although none is from the Kansas River Mainstream (Map 18). Within this basin the species varies considerably in abundance. Deacon and Metcalf (1961:316) found it to be the most abundant species at several stations, especially in the lower and middle parts, on tributaries to the mainstream of the Wakarusa River, but Minckley (1959:420) found only one specimen in an intensive survey of the fishes of the Big Blue River System. The only record outside the eastern part of the Basin is from Lenora, Kansas (Hay, 1887:249), on the North Fork of the Solomon River. I have examined these specimens (USNM 38232) and find them to be *N. umbratilis*. The westernmost records since that of Hay are: (1) KU 8133—Kans., Dickinson Co. at Rock Springs 4-H Camp, May 9, 1964 (20 specimens), (2) KU 8211—Kans., Dickinson Co., Lyon Cr., 3½ mi. northeast of Herrington, April 29, 1962, and (3) KU 8225—Kans., Morris Co., Clarks Cr., 4 mi. south and 2 mi. west of Skiddy, April 29, 1962 (1 specimen).

Variation and Zoogeography.—Hubbs and Ortenburger (1929b: 87) allocated specimens from the Arkansas and Red rivers in Arkansas and Oklahoma to *Notropis umbratilis umbratilis*. Males in breeding condition from the Kansas, Marais des Cygnes, and Arkansas river drainages in Kansas possess, in common, many small tubercles on the entire opercle, a character not shared by populations that I have examined from east of the Mississippi River nor by the specimen depicted by Trautman (1957:Fig. 79). Hubbs and Ortenburger (1929b:87) noted that the tubercles of *N. u. umbratilis* "cover the entire head." However, it seems unwise to assign specimens from the Kansas River Basin to *N. u. umbratilis* or another subspecies pending further study of this difficult group, the complexities of which are in need of thorough investigation.

Lack of penetration westward of this species and its widespread occurrence in the Ozark Region, suggest for western subspecies of *N. umbratilis* an area of origin in western tributaries of the Teays/Mississippi System draining the Ozark and Ouachita highlands and adjoining areas to the south. Possibly the fish was not present in the Ancestral Plains or Ancestral Missouri River drainages. Morphological adaptations suggestive of existence in the Great Plains are not clearly observable, although there seems to be a tendency towards a relatively larger head in progressing westward in both

the Arkansas River and Missouri River drainages (Table 12, unpublished, of doctoral dissertation by A. L. Metcalf, filed in Univ. Kansas Library, 1964).

Notropis cornutus (Mitchill)

Habitat and Distribution.—Collections made in the 1800's suggest that the northern common shiner then occurred widely in the Kansas River Basin (Map 19). Presently it seems to be restricted to two separate areas: (1) in streams draining the Flint Hills and Osage Cuestas and (2) in the headwaters of Smoky Hill River and possibly in the upper Republican River System in western Nebraska. Whether the species occurs naturally in the upper Republican is doubtful, as the only record is of three specimens (UMMZ 134375) taken from Champion Lake, Chase County, Nebraska, by R. E. Johnson on July 25, 1939. Champion Lake is an impoundment on Frenchman Creek.

In the Kansas River Basin, *Notropis cornutus* is almost restricted to clear, spring-fed creeks. Probably the siltation and other modifications that streams over much of the Basin have suffered due to agricultural practices have contributed to a reduction in range of this species. It may never have been common in the Glacial Till Plains and Loess Plains districts of the Basin. In the Stranger Creek System, for example, it is found only in areas where till has been removed and the underlying Oread Escarpment chiefly determines stream physiography. Cleary (1956:Map 44) indicated a similar scarcity of this species in the till plains of southeastern Iowa and Harlan and Speaker (1956:95) wrote, "This shiner has an ecological preference for clear water, and reaches its greatest abundance in the upstream tributaries to the major inland rivers. As collections progress downstream in the more turbid waters, the common shiner becomes reduced in numbers."

Zoogeography.—This species may have originated in Pliocene time according to Gilbert (1961:189). *N. cornutus* must have been at some time and to some degree isolated from the closely related *N. chrysocephalus* in order for speciation to take place. Since much of the unglaciated part of the Teays/Mississippi Drainage is presently occupied by the latter species, *N. cornutus* probably originated in a drainage to Hudson Bay or to the eastern, Atlantic Coast or both. That it did not originate in the Ancestral Plains Stream System is indicated by its limited penetration southwestward at the present time, and by the absence of fossils or historical records of this species in the southern Great Plains.

Notropis shumardi (Girard)

The synonymy, characters and distribution of the silver-banded shiner have recently been clarified and discussed by Gilbert and Bailey (1962). They map several localities of occurrence in the Missouri River from Missouri to South Dakota but none in the Kansas River System. I have seen only one specimen (MCZ 31885) from the Kansas River. This specimen is 37.0 mm in standard length and bears only the data "Topeka, Kansas." This specimen possesses eight anal rays (the anal fin is well-preserved); pharyngeal teeth are 2:4-4:2; the origin of the dorsal fin is only slightly behind that of the pelvic fin. Although the date of capture is not specified it seems that this was in the 1800's for the following reason: (1) the fish appears to have been preserved for a long time and (2) fishes taken in 1871 at Hays, Kansas, bear MCZ lot numbers close to that (18435) originally borne by specimen under consideration.

Notropis lutrensis lutrensis (Baird and Girard)

Distribution and Habitat.—The red shiner is one of the two most ubiquitous fishes in the Kansas River Basin—the other being *Pimephales promelas* (Maps 20 and 27). Almost every stream, large or small, from which collections exist has yielded this species. The only exceptions are headwater tributaries of the Big Blue River in Nebraska (Lincoln Creek and North Fork Blue River), which are exceedingly silty streams originating in an area mantled both by loess and glacial till (Fig. 2).

Zoogeography and Variation.—The red shiner is a species of the southern and southwestern Great Plains in terms of its present distribution, its preferred habitat, and its probable area of origin. Some of the environmental conditions that *N. l. lutrensis* tolerates in streams of the Great Plains are turbidity of water, silty and sandy bottoms, fluctuations in water level, intermittency, and extremes in water temperature (especially in shallow creeks of the High Plains). *N. lutrensis* is widespread in Atlantic Drainages of the southwestern United States and northern Mexico (Hubbs, 1940a: 6-9; Koster, 1957:67; Meek, 1904:72) and, as pointed out by Gibbs (1957:192), a southwestern origin seems likely for the "*lutrensis-ornatus*" group.

Presumably the Ancestral Plains Stream early received popula-

tions of *N. lutrensis* from the south. The species presently abounds in streams of the Great Plains as far north as the Platte System. In the Niobrara River it seems less common and it has not been taken in the western tributaries of the Missouri River in South Dakota, according to Bailey and Allum (1962:63). (The Preglacial Plains Stream System (Fig. 3) possibly extended no farther to the north than the present Platte Drainage.) From the hypothesized southwestern center of origin this species has not penetrated far eastward. In Iowa (Cleary, Map 49) it occurs widely in the southwestern part of the state but becomes rare northeastward. *N. lutrensis* was not found by Underhill (1957:18) in tributaries of the Mississippi River in Minnesota nor was it recorded from Wisconsin by Green (1935). In Illinois the species was interpreted by Forbes and Richardson (1909:144) as a "western" species. In Mississippi Cook (1958:112) reported it only from the Mississippi River Drainage.

Counts were made of the number of circumferential scales on series of *N. l. lutrensis* (10 per series) from the Platte, Kansas, and Arkansas river systems. The range of means for six series from the Platte was 25.9-26.7; for 14 series from the Kansas System 26.0-27.6 and for nine series from the Arkansas River in Kansas, western Oklahoma, and eastern Colorado 26.2-28.6. These figures suggest a slight increase in number of circumferential scales southward in the Great Plains. There were no discernible trends from east to west, however, in the streams considered. In the Kansas River Basin from east to west the following means were obtained: 26.4 — 26.9 — 26.0 — 27.5 — 26.3 — 26.8 — 26.9 — 27.4 — 27.6 — 26.5 — 26.9 — 27.3 — 26.3 — 27.5.

Notropis blennius (Girard)

Distribution and Habitat.—The distribution of the river shiner in the Kansas River System is disjunct (Map 21). It has been taken (1) in the mainstream of the Kansas River near Lawrence, Kansas, and (2) in the upper reaches of the Republican and Smoky Hill river systems in western Kansas and Nebraska. The species has been taken on several occasions in the Missouri River in Kansas and might, therefore, be expected to enter the lower part of the Kansas River. The distributional pattern of the upstream populations in certain shallow, clear streams resembles greatly

that of *Hybognathus hankinsoni*. *Notropis blennius* in the Missouri River System does not, however, possess the northern affinities of *H. hankinsoni* and, according to Bailey and Allum (1962:63), it is doubtful whether the species occurs in the System north of the Platte River.

The following specimens have been examined by me from the Kansas Basin (asterisk denotes presence of female distended by eggs in collection):

UMMZ 134345	(1)	Nebraska, Dundy Co., Republican River, July 24, 1939.
UMMZ 134366	(1)	Nebraska, Dundy Co., Rock Creek, July 24, 1939.
* UMMZ 135097	(2)	Nebraska, Red Willow Co., Republican River, July 17, 1940.
* UMMZ 135124	(6)	Nebraska, Dundy Co., Arikaree River, July 19, 1940.
* UMMZ 135133	(1)	Nebraska, Dundy Co., Arikaree River, July 19, 1940.
KU 1850	(1)	Kansas, Douglas Co., Kansas River at Lawrence, October 24, 1951.
KU 3787	(2)	Nebraska, Dundy Co., Arikaree River, April 29, 1947.
KU 4017	(1)	Kansas, Logan Co., Smoky Hill River, June 19, 1958.
MCZ 31881	(2)	Kansas, Shawnee Co., Kansas River at Topeka.

Zoogeography.—Recognition of two subspecies of *Notropis blennius* was proposed by Hubbs and Bonham (1951:103-107): *N. b. jejunus,* wide-ranging; *N. b. blennius* in a part of the Arkansas River System. Within the Arkansas River System, however, Hubbs and Bonham (p. 103) suggested the presence of *N. b. jejunus* in the Neosho (Grand) and Illinois Rivers in Oklahoma. Moreover, they found specimens (p. 103) "from Nebraska" to be intermediate between the two subspecies.

Knowledge concerning this species in the Great Plains is slight owing to the small number of specimens in collections. Analysis of four characters (Table 11) in which four western series were contrasted with three eastern series suggested, despite its cursory nature, that (1) eye size, although seemingly highly variable, may average slightly smaller in western populations, (2) the head is deeper and wider in the range of "*N. b. blennius*" in the Arkansas River System, and (3) southern and especially southwestern populations are deeper-bodied than northeastern populations.

Specimens from the Kansas River Basin seem intermediate between southwestern and northeastern populations. In addition to the characters listed above the anterior dorsal profile exhibits less

Table 11.—Measurements (Expressed as Thousandths of Standard Length) of Specimens of *Notropis blennius* (36-60 mm S. L.). Means Before Parentheses; Ranges Inside Parentheses.

Locality, Museum Number and Number of Specimens	Width of orbit	Length of head	Width of head	Greatest body depth
Nebraska, Hall County, Platte River (UMMZ 135209) (10)	63(60–66)	270(256–280)	140(130–147)	216(202–231)
Nebraska, Dundy and Red Willow Counties, Composite Coll., Kansas River Drainage (UMMZ and KU) (11)	67(62–72)	273(263–291)	143(134–152)	245(220–269)
Missouri, Platte County, Missouri River (KU 8242) (10)	77(70–80)	267(257–277)	147(142–152)	236(216–257)
Kansas, Cowley County, Arkansas River (UMMZ 127634 and KU 3669) (7)	70(63–73)	280(267–295)	153(147–162)	264(244–293)
Oklahoma, Payne County, Cimarron River at Ripley (UMMZ 113349) (9)	69(62–74)	282(270–301)	156(146–168)	258(237–274)
Wisconsin, Chippewa River, 5 miles SW Eau Claire (UMMZ 160320) (10)	71(62–79)	267(260–276)	137(121–143)	231(210–252)
Illinois, Mississippi River at Grand Tower (UMMZ 111587) (10)	80(74–82)	271(261–280)	143(137–156)	225(209–247)
Kentucky, Trigg County, Cumberland River (UMMZ 175023) (10)	75(71–79)	272(264–291)	144(137–153)	242(220–258)

decurvature than was observed in specimens from the Arkansas River System. The upper limb of the pharyngeal arch is broad, flattened, and smoothly curving anteriorly in specimens from the Kansas River. Specimens from Noble County, Oklahoma, have pharyngeal arches with the upper limb more rodlike and less smoothly curving anteriorly as described by Hubbs and Bonham (1951:104).

It seems impossible in this survey, because of insufficient material, to elucidate the subspecific status of several populations of this species.

It has been suggested that *Notropis braytoni* (Jordan and Evermann, 1896:264) and *Notropis potteri* (Hubbs and Bonham, 1951: 102) are allied to *Notropis blennius*. If such relationships are the fact this group of shiners seems marked by endemism in southwestern drainages. Within such a general pattern of endemism toward the Southwest, speciation in the direction of "*Notropis b. blennius*" as defined by Hubbs and Bonham could have been going on in the Arkansas River or possibly in the Ancestral Plains Stream System of an earlier time. If in the latter, upon deflection of western drainages into the central Mississippi Valley an eastern representative of the species, originally inhabiting the Teays/Mississippi, probably extended its range westward, invading the domain of the southwestern representative. There it intergraded extensively leaving evidence of the southwestern representative mainly in the southwestern part of the former Plains Stream System.

The pattern that seems to prevail here of a northern and eastern kind grading to a southwestern kind across the Kansas and Arkansas river systems suggests the pattern, discussed elsewhere, exhibited by *Pimephales promelas, Catostomus commersoni* and *Ictalurus melas.*

Notropis dorsalis (Agassiz)

To my knowledge, the only record of the big-mouthed shiner from the Kansas River Basin is of one specimen (KU 3479) taken from the Kansas River, Douglas County, Kansas (Sec. 5, T. 13 S, R. 21 E) on April 20, 1955.

The rarity of the species in the Kansas River Basin is difficult to understand because it is abundant in streams of southwestern Iowa, southeastern Nebraska and throughout most of the Platte River System.

The specimen taken from the Kansas River has the predorsal area

fully-scaled as do specimens from tributaries of the Missouri River in northeastern Kansas and from the Nemaha River System in southwestern Nebraska.

Notropis buchanani Meek

There are few records of the ghost shiner from the Kansas River Basin (Map 22). Minckley (1959:423), who first recorded the species from the Basin, caught two specimens (KU 3833), a female and a tuberculate male, along a sandbar in the lower part of the Big Blue River on August 14, 1957. Other specimens have been collected in the lower mainstream of Mill Creek in Wabaunsee County, Kansas. Deacon and Metcalf (1961:317) reported *N. buchanani* from the Wakarusa River, basing their record on two specimens collected by C. W. Creaser in 1924 (UMMZ 63107).

The ghost shiner seems to be restricted to the eastern part of the Basin, where it is rare. Hubbs and Ortenburger (1929b:68), Metcalf (1959:367), and Deacon (1961:382) discussed the predilection of this species for larger streams over smaller tributaries in Oklahoma and southeastern Kansas; Deacon found it to prefer relatively quiet water adjacent to the strong current of the mainstream. Seemingly it has entered the Kansas River Basin from the southeast.

Notropis heterolepis Eigenmann and Eigenmann

There are no records, known to me, of the black-nosed shiner from the Kansas River Basin. The only basis for its inclusion in the fauna is Hubbs' (1951a) interpretation of *Notropis germanus* Hay from the Smoky Hill River at Wallace as a hybrid between *N. heterolepis* and *Hybognathus hankinsoni*. As pointed out by Hubbs (1951a:451), *N. heterolepis* probably once occurred in the Kansas River Basin. The species has been taken in recent years in Missouri, downstream from the mouth of the Kansas River, and it is known to have existed in the Missouri River Drainage of South Dakota (Bailey and Allum, 1962:70), Iowa (Harlan and Speaker, 1956:98), Nebraska (Evermann and Cox, 1896:401) and Colorado (Ellis, 1914:49) in former times; thus it might easily have had access to the Kansas River Basin. Extirpation over much of the southern part of the former range of the species has been discussed by Hubbs (1951a:451), Cleary (1956:272), and Trautman (1957: 388-390). As noted by Hubbs (1951a:451) the specimens (UMMZ 167085, USNM 69382, 69383), reported by Jordan (1891:17, 18) as

Notropis cayuga from the Arkansas River at Wichita, Kansas, are *N. heterolepis*. Thus, barring an error in locality data, the range of this shiner once extended south to the Arkansas River Drainage. If this be true the species probably gained access to the Arkansas Drainage from the north by way of its former connections with the Ancestral Plains Stream.

Notropis stramineus missuriensis (Cope)

Habitat and Distribution.—The sand shiner is one of the most abundant and widespread species of the Kansas River Basin (Map 23). It has been collected from approximately 200 localities in the Basin and is exceeded in its ubiquity only by *Pimephales promelas* and *Notropis lutrensis*. Although taken in many kinds of streams, large and small, it was most common over sandy bottoms.

Variation and Zoogeography.—Bailey and Allum (1962:64-68) found two subspecies of the sand shiner in South Dakota—a small-scaled subspecies (*N. s. missuriensis*) generally west of the Missouri River and a large-scaled subspecies (*N. s. stramineus*) east of the Missouri. The two subspecies were found to intergrade over a narrow zone in that state. Southward in the Great Plains a similar situation seems to prevail (see Table 12, which has the same format as that used by Bailey and Allum, Table 15, for ease of comparison).

Populations from the Kansas and Platte rivers seem assignable to *Notropis s. missuriensis* (circumferential scales averaging 26.3-29.4; predorsal scales averaging 16.0-18.5 in the western parts of the basins to 15.0-17.0 in the eastern parts). Although some populations of the Big Blue River System in Kansas were considered intergrades by Minckley (1959:423), intergradation in that stream and in other streams in the eastern part of the Kansas River System is slight and mosaic in nature. Intergrading populations inhabit other tributaries of the Missouri River south of the mouth of the Platte and eastward at least to and including the Chariton (Bailey and Allum, 1962:64) and Blackwater rivers in Missouri (circumferential scales averaging 24.9-25.7; predorsal scales 14.4-15.1. In the Moreau, Osage, and Gasconade systems and eastward in the Missouri River System *N. s. stramineus* occurs (circumferential scales averaging 23.0-24.5; predorsal scales 12.9-13.6). The geographical pattern of intergradation in these areas resembles that between subspecies of the orange-throated darter—*Etheostoma s. spectabile* and *E. s. pulchellum*.

In the Arkansas River System relationships similar to those noted above exist. West of the Verdigris River System, *N. s. missuriensis* occurs through Kansas, Oklahoma, Colorado and New Mexico (circumferential scales averaging 28.7-30.7; predorsal scales 16.0-17.5). In the Neosho River System of Kansas, however, intergrading populations are found (circumferential scales, 24.9-25.5; predorsal scales 13.4-14.2). The pattern of intergradation in northeastern Oklahoma and Arkansas has not been investigated by me.

Sand shiners from the Red River (of the south) have been referred to "*Notropis d. deliciosus*" by Hubbs and Ortenburger (1929a:28) and Hubbs and Lagler (1958:84). Specimens that I have examined from the Red River Drainage of eastern and central Oklahoma have the large scales of *N. s. stramineus* (circumferential scales averaging 23.8-24.4; predorsal scales 12.9-14.3); however, series from the North Fork Red River in southwestern Oklahoma give evidence of intergradation with *N. s. missuriensis* (circumferential scales averaging 25.5-26.2; predorsal scales 14.3-14.4).

A few specimens examined from the Colorado River System of Texas and the Río Grande System in Coahuila, Mexico, have the large scales of *N. s. stramineus.* Circumferential scales averaged 23.6 and predorsal scales 13.5 for eight specimens from the Colorado Drainage. Circumferential scales averaged 23.7 and predorsal scales 14.2 for 23 specimens from the Río Grande Drainage.

The subspecies *N. s. missuriensis* seems especially tolerant of (adapted to) rivers of the Great Plains. Probably its squamation exemplifies such an adaptation. In addition to possessing smaller scales westward, occasional individuals or, in some collections, a large percentage of specimens, have embedded scales predorsally or lack scales on the nape. As *N. s. missuriensis* occurs in the Arkansas River and other Plains streams to the north, and as it varies little from stream to stream, it probably dispersed throughout this region when streams formed an integrated drainageway (Ancestral Plains Stream) (Figs. 3 and 4). The presence of intergradational populations in the western part of the Red River System suggests that it has had connections to the drainageway mentioned above, but that these connections were less intimate or less recent than those between streams to the north. Subsequent to deflection of the upper Kansas River eastward the plains subspecies penetrated slightly to the east in the lower Kansas and Platte river basins and adjacent parts of the Missouri River System where intergrades now occur.

Table 12.—Frequency-distribution of Circumferential Scale-counts in Some Specimens of *Notropis stramineus* (Cope) From the Great Plains and Interior Lowlands

Drainage and Locality (Museum No. in Parenthesis)	Body-circumference scales														No.	Mean
	21	22	23	24	25	26	27	28	29	30	31	32	33	34		
Lower Missouri River Drainage:																
Mo., Montgomery Co., Clark's Br. (KU 8214)	....	3	6	9	1	1	....	....	....	....	....	....	....	....	20	23.6
Mo., Boone Co., Cedar Cr. (KU 8215)	....	1	1	13	2	3	....	....	....	....	....	....	....	....	20	24.3
Mo., Osage Co., Gasconade R. (KU 5162)	....	1	2	12	3	....	....	....	....	....	....	....	....	....	18	23.9
Mo., Hickory Co., Pomme de Terre R. (KU 7815)	....	....	1	16	2	1	....	....	....	....	....	....	....	....	20	24.2
Mo., Cole Co., Moreau Cr. (KU 8216)	....	1	8	8	3	....	....	....	....	....	....	....	....	....	20	23.7
Mo., Henry Co., Osage R. (USNM 36222)	1	5	3	5	1	....	....	....	....	....	....	....	....	....	15	23.0
Ks., Bourbon Co., Drywood Cr. (KU 3580)	....	....	3	8	6	2	1	....	....	....	....	....	....	....	20	24.5
Ks., Miami Co., Little Wea Cr. (KU 4700)	....	....	1	16	3	....	....	....	....	....	....	....	....	....	20	24.1
Ks., Doniphan Co., Missouri R. (KU 7331)	....	....	....	10	4	1	3	2	....	....	....	....	....	....	20	25.2
Ks., Atchison Co., Deer Cr. (KU 7321)	....	....	....	7	8	1	3	....	....	....	....	....	....	....	19	25.0
Ks., Brown Co., Wolf Cr. (KU 5387)	....	....	....	4	5	3	1	....	....	....	....	....	....	....	13	24.9
Nebr., Richardson Co., Trib. of S. Fk. Nemaha R. (KU 7146)	....	....	2	5	2	3	5	2	1	....	....	....	....	....	20	25.7

Nebr., Otoe Co., Trib. of N. Fk. Nemaha R. (KU 7148)			1	5	7	2		4	1						20	25.5
Platte River Drainage (east to west):																
Nebr., Dixon Co., Logan Cr. (KU 7157)				2	4	2	6	5		1					20	26.6
Nebr., Holt Co., Elkhorn R. (KU 7177)				1			4	5							10	27.2
Nebr., Thomas Co., Dismal R. (KU 7108)				1			6	11	2						20	27.6
Nebr., Keith Co., N. Platte R. (KU 4847)				1	1	3	4	7	2	2					20	27.5
Nebr., Banner Co., Pumpkin Cr. (KU 4829)					1	3	2	10	2	2					20	27.8
Colo., Logan Co., S. Platte R. (KU 4671)				2	1	2	7	3	3	2					20	27.3
Colo., Larimer Co., Cache la Poudre R. (KU 5566)				4	3	5	3	2	3						20	26.3
Wyo., Platte Co., N. Laramie R. (KU 4815)				2	1	2	8	6	1						20	27.0
Kansas River Drainage (east to west):																
Ks., Jefferson Co., Walnut Cr. (KU 8204)					1	2	3	7	5	2					20	28.0
Ks., Douglas Co., Spring Cr. (KU 4695)					2	3	1	5	2	1	1				15	27.6
Ks., Jefferson Co., Honey Cr. (KU 7316)						1	1	11	5	1	1				20	28.4
Ks., Brown Co., Cedar Cr. (KU 8234)						1	4	9	4	2					20	28.1
Ks., Shawnee Co., Shunganunga Cr. (KU 1955)				2		5	4	5	2	1	1				20	27.1

Table 12.—*Continued*

Drainage and Locality (Museum No. in Parenthesis)	Body-circumference scales														No.	Mean
	21	22	23	24	25	26	27	28	29	30	31	32	33	34		
Kansas River Drainage (east to west): —*Concluded*																
Ks., Pottawatomie Co., Carnahan Cr. (KU 4186)	....	....	....	....	3	5	6	2	3	1	....	....	....	....	20	27.0
Ks., Morris Co., Clarks Cr. (KU 8223)	....	....	....	1	4	....	2	8	4	1	....	....	....	....	20	27.4
Ks., Dickinson Co., Lyon Cr. (KU 8212)	....	....	....	1	2	4	4	7	2	....	....	....	....	....	20	27.0
Ks., Washington Co., Little Blue R. (KU 4385)	....	....	....	....	4	4	4	6	1	1	....	....	....	....	20	27.0
Ks., McPherson Co., Gypsum Cr. (KU 8239)	....	....	....	....	1	1	4	8	1	3	1	....	....	....	19	28.1
Nebr., Adams Co., Little Blue R. (KU 8228)	....	....	....	4	1	2	6	2	2	2	1	....	....	....	20	27.0
Ks., Clay Co., Peet Cr. (KU 7059)	....	....	....	....	....	1	1	9	6	2	1	....	....	....	20	28.5
Nebr., Webster Co., Elm Cr. (KU 7053)	....	....	....	....	1	1	2	3	3	....	....	....	....	....	10	27.6
Nebr., Franklin Co., Cottonwood Cr. (KU 7035)	....	....	....	....	1	2	4	5	4	2	1	1	....	....	20	28.2
Ks., Trego Co., Saline R. (KU 3986)	....	....	....	2	3	2	4	4	3	2	....	....	....	....	20	27.1
Ks., Norton Co., Prairie Dog Cr. (KU 5571)	....	....	....	....	....	....	1	5	7	4	1	1	....	1	20	29.4

Ks., Wallace Co., Rose Cr. (KU 4028)					2	4	7	1	4		1	1			20	27.5
Nebr., Dundy Co., S. Fk. Republican R. (KU 7130)						3	2	5	6	2	2				20	28.4
Arkansas River Drainage (east to west): Ks., Labette Co., Neosho R. (KU 3207)				5	4	2	2	2							15	25.5
Ks., Neosho R. (Composite, Coffey to Labette Counties)			5	5	4	3	2	1							20	24.9
Ks., Lyon Co., Neosho R. at Neosho Rapids (KU 2550)				3	5	2		1							11	25.2
Ks., Upper tributaries of Neosho R. (Composite)				7	4	5									16	24.9
Ks., Cowley Co., Arkansas R. (KU 4150)							2	6	4	5	3				20	29.1
Okla., Garfield Co., Black Bear Cr. (OAM 1638)						1	1	1	1	6	1	1			12	29.4
Ks., Pratt Co., S. Fk. Ninnescah R. (KU 3934)						2	2	5	3	2	3	2	1		20	29.2
Ks., Kiowa Co., Medicine R. Dr. (KU 1261)							1	5	9	5					20	28.9
Ks., Ford Co., Arkansas R. (KU 3943)								3	3	2	5	4	2	1	20	30.7
Ks., Meade Co., Spring Cr. (KU 3947)								1	3	4	5	7			20	30.7
Ks., Hamilton Co., Arkansas R. (KU 5556)						1	1	5	9		2		2		20	29.1
Okla., Cimarron Co., Trib. of Cimarron R. (KU 3798)						2	2	2	2	5	6		1		20	29.5

TABLE 12.—*Concluded*

DRAINAGE AND LOCALITY (Museum No. in Parenthesis)	Body-circumference scales														No.	Mean
	21	22	23	24	25	26	27	28	29	30	31	32	33	34		
Arkansas River Drainage (east to west): —*Concluded*																
Colo., Prowers Co., Arkansas R. (KU 4739)	....	....	....	....	1	2	2	3	5	5	1	1	....	....	20	28.7
Colo., Pueblo Co., Arkansas R. (KU 4751)	....	....	....	....	....	1	....	4	5	8	2	....	....	....	20	29.3
N. M., Mora Co., Mora R. (KU 4231)	....	....	....	....	....	....	....	....	4	4	1	1	....	....	10	29.9
Red River Drainage (east to west):																
Okla., Pontotoc Co., Clear Boggy R. (OAM 1610, 2373)	....	....	2	13	5	2	1	....	....	....	....	....	....	....	23	24.4
Okla., Pontotoc Co., Blue R. (OAM 1579)	....	1	1	8	3	3	....	....	....	....	....	....	....	....	16	24.4
Okla., Johnston Co., Blue R. (OAM 160, 2088)	....	....	3	3	....	1	1	....	....	....	....	....	....	....	8	24.3
Okla., Murray Co., Washita R. Drainage (OAM 2228, 2264, 5349)	....	3	16	38	6	....	....	....	....	....	....	....	....	....	63	23.8
Okla., Custer Co., Beaver Cr. (Washita R. Dr.) (KU 8045)	....	....	2	5	1	....	....	....	....	....	....	....	....	....	8	23.9
Okla., Beckham Co., Timber Cr. (N. Fk. Red R. Dr.) (KU 8054)	....	....	....	1	8	2	6	2	1	....	....	....	....	....	20	26.2

Okla., Beckham Co., North Fork Red R. at Sayre (KU 8098)	....	....	....	5	7	4	2	2	....	....	....	....	....	....	20	25.5
Colorado River Drainage:																
Texas, Hays Co., Blanco R. at Wimberly (KU 5996)	....	....	3	5	....	....	....	....	....	....	....	....	....	....	8	23.6
Rio Grande River Drainage:																
Mexico, Coahuila, 1 mi. NW El Moral (KU 2982)	....	....	2	1	1	....	....	....	....	....	....	....	....	....	4	23.8
Mexico, Coahuila, San Diego R., 2 mi. W Jimenez (KU 3006, 3020, 3034)	....	....	7	10	2	....	....	....	....	....	....	....	....	....	19	23.7

Notropis topeka (Gilbert)

Distribution and Habitat.—The Topeka shiner seems, at the present time, to be almost restricted to streams draining the Flint Hills and the Oread Escarpment in the Kansas River Basin (Map 24). The only record outside these areas since 1900 is a specimen (KU 3108) taken by A. B. Leonard and A. B. Williams from Cherry Creek, Cheyenne County, Kansas in 1947. Prior to 1900 there were several records of the species from the western part of the Drainage (Gilbert, 1884, 1885a, 1885b, 1886, 1889; Cragin, 1885b; Hay, 1887).

The distribution, habitat and abundance of *N. topeka* in Kansas have been discussed by Minckley and Cross (1959). They found evidence that this species increased in abundance in streams of the Flint Hills during a period of drought (in 1956) marked by lowering of water level and intermittency. Conversely, they found that as years of greater rainfall returned (1957-58) that spawning by *N. topeka* seemed less successful than that of other species of minnows in the same streams.

Minckley and Cross (1959:215-216) suggested that *N. topeka* may have been rare in streams of the Flint Hills prior to and at the time of settlement noting "In Kansas, it seems that the Topeka Shiner has almost disappeared from areas other than the Flint Hills but has increased in abundance in that area."

The pattern of distribution and of extirpation of *N. topeka* resembles greatly that of *Notropis cornutus*, *Chrosomus erythrogaster*, and *Hybopsis biguttata*, which are interpreted elsewhere as species that were once more widely distributed in the clearer streams of the Basin including the Flint Hills and Shawnee Escarpments area but are now almost restricted to these areas as they possess the best remaining habitat.

Zoogeography.—The zoogeography of the Topeka Shiner is puzzling. Its absence east of the Mississippi River is notable. Its western distribution (Bailey and Allum, 1962: Fig. 6) suggests an origin in the Pleistocene south-draining master stream of the Great Plains that integrated at one time or another parts of the present Arkansas, Kansas, Platte and upper Missouri systems. The species still occurs in and reaches its greatest abundance in these systems. From such a center of origin I envisage a modest invasion by this headwater species eastward, as suggested by Bailey and Allum (1962:125), into the upper parts of the Des Moines, Iowa and Cedar rivers (Underhill, 1957:19; Cleary, 1956: Map 51;

Bailey, 1959:120). Such an invasion almost certainly occurred by headwater transfer subsequent to the retreat of the Wisconsinan glacier (the distribution in Iowa of this fish is restricted to areas glaciated in the Wisconsinan Age). Thus the dispersal northeastward is of recent occurrence and might easily have been accomplished by a fish with the strong preferences for shallow headwater streams suggested by Minckley and Cross (1959:211-212). "Tributary hopping" in an eastward direction may have taken place along the Missouri River in Missouri as populations are found in short tributaries on both sides of Missouri River as far east as Gasconade County (Bailey and Allum, 1962: Fig. 6; Fisher, 1962:427).

Bailey (1959a:120) pointed out certain anatomical resemblances between *N. topeka* and *Notropis anogenus* Forbes. Possibly an ancestral stock gave rise to *N. topeka* in the Ancestral Plains Stream and to *N. anogenus* in a north-central drainage of the Mississippi Valley, such as the Driftless Area centered in Wisconsin. As pointed out by Bailey (1959a:120) the two species were probably sympatric in southern Minnesota and north-central Iowa prior to settlement of the land. However, invasion of this glaciated area by these forms could only have occurred in post-Wisconsinan time.

Hybognathus hankinsoni Hubbs

Habitat and Distribution.—The brassy minnow seems rare in the Kansas River Basin (Map 25). I know of only ten records as indicated below. All are from cool creeks of the western or High Plains section of the Basin. These creeks are fed by springs issuing either from the contact of the Ogallala Formation and the underlying, aquicluding Cretaceous rocks or from aquiferous Pleistocene gravels of the Holdrege or Grand Island formations or both. Elsewhere in Kansas this species is known only from one small but permanent, direct tributary of the Missouri River in Atchison County.

UMMZ 66144	(5)	Colorado, Yuma Co., Arikaree River at Beecher's Island, October 10, 1915.
UMMZ 134328	(3)	Nebraska, Lincoln Co., Medicine Creek, July 23, 1939.
UMMZ 134361	(7)	Nebraska, Dundy Co., Rock Creek, July 24, 1939.
UMMZ 160450 160462		Kansas, Wallace Co., Rose Cr. and South Fork Smoky Hill River, (2 mi. S, 2 mi. west of Wallace) July 26, 1950.
USNM 38237	(1)	Kansas, Wallace Co., Smoky Hill River at Wallace, July, 1885 (O. P. Hay).

KU 2680	(7)	Nebraska, Dundy Co., Arikaree River, 3 miles W. Haigler, November 1, 1952.
KU 3788	(4)	Kansas, Sherman Co., North Branch, Smoky Hill River (Sec. 13, T. 10 S, R. 40 W), April 28, 1947.
KU 4043	(1)	Kansas, Cheyenne Co., Republican River, (Secs. 16 and 17, T. 4 S, R. 41 W) June 21, 1958.
KU 4859	(2)	Nebraska, Hitchcock Co., Frenchman Creek, below Enders Reservoir, September 11, 1959.
KU 7039	(1)	Nebraska, Franklin Co., Cottonwood Creek, 1 mile W. Bloomington, July 10, 1961.

These few, isolated records suggest that *H. hankinsoni,* mainly northern in its present distribution, is a relict in the Kansas River Basin. That it occurred farther south in southwestern Kansas in Illinoian time has been pointed out by G. R. Smith (1963:279).

Zoogeography.—This minnow's rarity in the Basin contrasts with its status in Minnesota, where Underhill (1957:20) judged it to be probably the most abundant minnow in the state.

Much of the range presently occupied by *H. hankinsoni* (as mapped by Bailey, 1954:290) was glaciated once or two or more times in the Wisconsinan Glacial Stage. Bailey's (1954:291) speculation that the fish invaded these glaciated areas from refugia in the upper Missouri and upper Mississippi River systems seem logical. Its absence in the Ohio River Valley suggests that the species evolved in a drainage far from and/or not intimately connected to the Ohio. Its widespread distribution in the upper Missouri Basin and its occurrence in beds of Illinoian age in southwestern Kansas (G. R. Smith, 1963:279) suggest a possible origin in a western drainage such as the ancestral north-flowing Missouri or the Ancestral Plains Stream or both.

Hybognathus placitus Girard

Distribution and Habitat.—Most records for the plains minnow from the Kansas River Basin are unreliable due to confusion concerning the specific distinctness of *H. placitus* and *H. n. nuchalis. H. placitus* occurs widely in the Kansas River Basin (Al-Rawi and Cross, 1964:164, 165); *H. n. nuchalis* has been found only in the lower mainstream. Al-Rawi and Cross (1964:163) aptly characterized the habitat of *H. placitus* as ". . . shallow, silty water adjacent to shifting sand-bottoms of the larger prairie streams that have low gradients." Trautman (1957:397) noted that in the Ohio River Bason *H. n. nuchalis* eschewed streams with silty bottoms and turbid water.

Zoogeography.—Of the three major pre-glacial drainages described previously (Fig. 3) the ancestral Plains Stream probably

harbored *H. placitus* and the ancestral Teays/Mississippi and possibly some other streams of the Atlantic and Gulf coasts harbored *H. n. nuchalis.* This is suggested by the present range of *H. placitus* throughout most of the length and breadth of the Great Plains. With Pleistocene disruption and diversion of these drainages and incorporation of parts of both into the present Missouri River System both species had access to the Kansas River Basin. Even today the distribution and habitat preferences exhibited by the two species in the Kansas River System betoken a Plains origin and an eastern origin.

Hybognathus nuchalis nuchalis Agassiz

The silvery minnow occurs in the lower part of the Kansas River Mainstream. Probably it does not penetrate far to the west; however, its distributional pattern is not clear, because of former confusion of this species with *Hybognathus placitis.* Habitat preferences and zoogeography of the two species have been discussed above in the account of *H. placitus.*

Pimephales notatus (Rafinesque)

Habitat and Distribution.—The blunt-nosed minnow reaches its greatest abundance in the Kansas River Basin in clear creeks having high gradient and rubbly bottoms in the Shawnee Escarpments and Flint Hills. West and north of this area of concentration there are only scattered records and none at all from the entire Republican River System (Map 26). Specimens that I have seen, representing peripheral records, are indicated below together with collectors and year of collection.

KU 3977	Kansas, Ellis Co., Ellis, Big Creek—F. B. Cross and Bernard Nelson, 1958.
KU 3981	Kansas, Trego Co., Saline River—F. B. Cross and Bernard Nelson, 1958.
UMMZ 160471	Kansas, Logan Co., 8½ mi. W. Russell Springs, S. Fk., Smoky Hill River—W. R. Taylor and H. Hildebrand, 1950.
USNM 37939	Kansas, Norton Co., Lenora, N. Fk., Solomon River—O. P. Hay, 1886.
USNM 37955	Kansas, Phillips Co., Kirwin, N. Fk., Solomon River—O. P. Hay, 1886.
USNM 68214	Nebraska, Saline Co., Crete, Blue River—S. E. Meek, 1891.

Zoogeography.—In western tributaries of the Missouri River, north of the Kansas River, *P. notatus* is recorded only from the Elkhorn River (Meek, 1894:136—MCZ 31845). Its absence in so large a part of the Missouri Basin reflects scarcity of habitat suitable

for blunt-nosed minnows. *P. notatus* probably has little ability to penetrate the many miles of monotonous, sandy mainstream that intervene between rubble-bottomed tributaries.

The blunt-nosed minnow probably entered the Kansas River Basin from the southeast; the species is common in the Ozark Region and eastward. Bailey and Allum (1962:76) speculated that populations in Missouri River tributaries in eastern South Dakota entered that area from the upper Mississippi River System.

Pimephales promelas Rafinesque

Habitat and Distribution.—The fat-headed minnow is the most widespread species occurring in the Kansas River Basin. It has been taken at approximately 240 localities in all kinds of streams (Map 27). A number of records prior to 1900 from both the eastern and western parts of the Basin are available.

Northward from the Kansas River in the Missouri River Basin *P. promelas* is also abundant. Bailey and Allum (1962:77) found it to be "probably the most ubiquitous fish in South Dakota." Southward from the Kansas River in the Arkansas River System the species seems generally less abundant.

Variation and Zoogeography.—Hubbs and Ortenburger (1929a: 38) and Taylor (1954:42) noted differences between populations of fat-headed minnows from north-central and southwestern (Oklahoma and Texas) states. These differences prevail from north to south in the Great Plains. Populations from the Platte River Drainage northward differ from populations in the Arkansas River and southward into Mexico, as pointed out by Hubbs and Ortenburger (1929a:38); populations from the Kansas River Basin are intergradational between the two. Northern populations in the Great Plains (Platte and Nemaha rivers northward) have fewer pored scales in the lateral line and more head-tubercles (especially on the chin) than do southern specimens. In addition, the northern representatives possess slightly fewer circumferential scales and have a slenderer body form, with less decurvature of the anterior profile and a less chubby head.

The diversity between southwestern and northern populations has been given taxonomic status by recognition of a southwestern representative called *Pimephales promelas confertus.* However, I follow Taylor (1954) and Bailey (1956:328) in utilizing only the binomial. The geographic variation of *P. promelas* is currently being studied by John Vandermeer, University of Kansas.

The differences between representatives of the species from the southern and northern Great Plains might be attributed to one or more of the following: 1) Direct effect of environment in producing different phenotypes; 2) Influence of a stock lingering in the upper Missouri Basin from the fauna of the preglacial north-flowing Missouri River; or 3) Invasion of a stock originating in the Teays/Mississippi into the middle and upper Missouri River System. *P. promelas,* a widespread species (Canada to Mexico) seemingly tolerant of a wide range of temperatures and water conditions, possibly occupied all three preglacial drainages discussed herein (Fig. 3), and populations in the Missouri River Basin may be a melange, resulting from mixing of two or three stocks.

Campostoma anomalum pullum (Agassiz)

Habitat and Distribution.—The central stoneroller is distributed throughout the Kansas River Basin, but is rare or absent in areas where thick glacial till or loess is deposited and in other areas where siltation of streams is extreme (Map 28). Thus, it is absent in the Loess Hills (Fig. 2) north of the Republican River in south-central Nebraska (Medicine Creek and Red Willow Creek) and in the upper part of the watershed of the Big Blue River in Nebraska. It is uncommon in the glacial till-plains in Kansas and Nebraska (in collections made by R. E. Johnson and by myself). In Iowa, Cleary (1956:Map 59) showed it to be almost absent from the till-plains south of the Wisconsinan end-moraines in southwestern Iowa. In Illinois, Forbes and Richardson (1909:111) found the stoneroller to be among those fishes that assiduously avoided till-plains of the area covered by glaciers of Illinoian age. The species is most common in clear streams with bottoms of rubble, gravel or coarse sand. It prefers smaller creeks in the Kansas River Basin, often ascending to their ultimate headwaters. In the western part of the Basin it is most common in the area fed by springs issuing from Pleistocene gravel deposits or from the contact of the Ogallala Formation with underlying beds of Cretaceous age.

Variation and Zoogeography.—Stonerollers from parts of the Kansas River Basin have been assigned to the subspecies *plumbeum* by Breukelman (1940a:371) and by Minckley (1959:426), but the distinguishing characters of *plumbeum* were not well defined by anyone including Girard (1856:178; 1858:228, 229) who proposed the name "*Dionda plumbea*" and it remained for Hubbs and Ortenburger (1929b:95) to show that *D. plumbea,* together with

Dionda spadicea Girard and *Dionda grisea* Girard, was conspecific with *Campostoma anomalum* (Rafinesque). Hubbs and Ortenburger (1929b:95) did not specifically propose use of the trinomial.

Subspecific allocations in *Campostoma anomalum* have been made chiefly on the basis of the number of scales in the lateral line and around the body. Counts of lateral line and circumferential scales were made (unpublished tables 15 and 16 of doctoral dissertation by A. L. Metcalf, filed in Univ. Kansas Library, 1964) on 40 series of stonerollers from the Great Plains and on the types of *Chondrostoma pullum* Agassiz (UMMZ 86455). Specimens (PAS 5066) labeled "Cotype of *Dionda plumbea* Girard. Headwaters of the Canadian River (Llano Estacado). H. B. Mollhausen. Smiths. Inst. (2981) 5066" are too poorly preserved to allow reliable counts to be made.

Although populations from the Kansas River Basin and from some other parts of the Great Plains possess, on the average, higher circumferential scale-counts than those reported for some populations of *C. a. pullum* to the east and north, the differences seem gradational from one area to the other. Following the reasoning of Bailey, Winn and Smith (1954:148-149) I think it judicious not to recognize subspecies of fishes where differences are clinal and of slight degree from one geographic area to another. In this case the cline involving squamation is poorly defined from east to west and in some places seems to be disrupted or even reversed. In the Arkansas River Basin, however, there is a recognizable cline toward decreasing size of scale from east to west. Confounding the expression of an east-west cline may be a north-south cline. Specimens from the upper Platte River have consistently lower scale-counts than do specimens from the adjacent upper Arkansas River in Colorado.

Subspecific partitioning of populations of the central stoneroller into *pullum* and *plumbeum* seems to me to obscure the basic unity of morphology which distinguishes this wide-ranging kind and which sets it off from the coarse-scaled stoneroller (*C. anomalum oligolepis*). In the case of *C. a. pullum* and *C. a. plumbeum* the degree of difference is slight and involves, so far as has been pointed out, only clinal differences in scale size. In *C. a. pullum* as compared with coarse-scaled stonerollers there are trenchant differences not only in scalation but also in body-proportions, shape of mouth, tubercle-patterns and breeding coloration.

Greene (1935:132) suggested that *C. a. oligolepis* had its origin in the Driftless Area, centered in Wisconsin, whereas *C. a. pullum* originated in the Mississippi River Valley to the south of the Driftless Area. However, the subsequent discovery that *C. a. oligolepis* also occurs in the Ozark Region and the fact that much of the Ohio River Basin is populated by a related, coarse-scaled stoneroller (*C. a. anomalum*) makes Greene's hypothesis untenable and argues for an original (possibly preglacial) habitation by coarse-scaled stonerollers of the Teays/Mississippi System. Ancestral stock of the central stoneroller must have originated west, south or southwest of the main part of the Teays/Mississippi Basin. That fine-scaled members of the genus have long inhabited southwestern drainages is suggested by the presence of *C. ornatum,* extreme in regard to smallness of scales, in a part of the Rio Grande Drainage and in some other drainages of northern Mexico. Areas of origin for stock of the central stoneroller might have included one or more of the following: (1) Ancestral Plains Drainage, (2) Ouachita Mountains, and (3) coastal streams of Texas and Louisiana. That the Ancestral Plains Drainage was among areas early inhabited by the central stoneroller is suggested by fossils that possess, according to G. R. Smith (1963:279), dentaries that "are referable to the narrow-jawed subspecies, *C. a. pullum* (Agassiz) of the Mississippi Valley or *C. a. plumbeum* (Girard), of the High Plains, on the basis of the narrow gnathic ramus . . ." The penetration of the central stoneroller eastward into certain Atlantic Coast-drainages of New York and into the upper Allegheny River (Ross, 1958:3) suggests that its invasion northeastward has long been in progress, possibly dating from one or more Pleistocene interglacial stages.

Cycleptus elongatus (LeSueur)

I have seen no specimens of the blue sucker from the Kansas River Basin other than KSU 2917, collected by I. D. Graham from the Blue River, probably in the 1880's and discussed by Minckley (1959:416). *C. elongatus* was listed by Graham (1885a:72; 1885b) from "Kansas River." Cragin (1885b:107) specified "Neither rare nor abundant in Kansas R. I have known of a fisherman taking twenty specimens or thereabout in a trip from Manhattan to Topeka." As misidentification of this distinctive fish is unlikely it must be assumed that the absence of more recent records than those just quoted indicates a marked depletion in numbers of this species

in the Kansas River. However, as it penetrates as far north in the Missouri River as Iowa (Harlan and Speaker, 1956:71) and South Dakota (Bailey and Allum, 1962:78) it doubtless still enters the lowermost Kansas River on occasion.

Ictiobus cyprinellus (Valenciennes)

Distribution and Habitat.—The big-mouthed buffalo is abundant in the lower mainstream of the Kansas River and in the downstream parts of major tributaries such as the Wakarusa River (Deacon and Metcalf, 1961:315). It seems to range farther upstream than the other species of *Ictiobus* (Maps 29 and 30).

Ictiobus bubalus (Rafinesque)

The small-mouthed buffalo occurs commonly in the larger streams of the lower part of the Kansas River Basin (Map 30). Many of the specimens examined by me are young fish and are difficult to separate from *Ictiobus niger*. For specimens more than 20 cm in standard length, values for height of anteriormost dorsal ray divided by head length ranged from .85 to 1.07 (see Trautman, 1957:226).

Ictiobus niger (Rafinesque)

The black buffalo seems rare in the Kansas River Basin, although its rarity may reflect only inadequate sampling of the larger waters. It is much less common in collections than either *I. bubalus* or *I. cyprinellus*. I have examined only four specimens, all mature, from the Basin in Kansas as follows: KU 3134 and 3135 from Douglas County at Lakeview, an oxbow lake south of the Kansas River; KU 3912 from the Big Blue River, Riley County, and KU 4373 from the Little Blue River, Marshall County. Values for length of anteriormost dorsal ray divided by head length ranged from .64 to .71 for these specimens.

Carpiodes cyprinus (LeSueur)

Habitat and Distribution.—Records of the quillback from the Kansas River Basin are two few to allow much insight regarding its choice of habitat; however a preference may exist for the shallow, sandy streams of the central and western parts of the Basin. Specimens that I have seen are listed below:

UMMZ 135904 (3) Nebraska, Red Willow Co., Republican River, 1 mi. S. Indianola, July 17, 1940.

UMMZ 135121	(1)	Nebraska, Dundy Co., Arikaree River, July 19, 1940.
KU 4180	(1)	Kansas, Riley Co., Big Blue River, June 20, 1940.
KU 4864	(1)	Nebraska, Furnas Co., Republican River at Cambridge, September 12, 1959.
KU 7136	(1)	Nebraska, Dundy Co., South Republican River, August 23, 1961.
PAS 89957	(2)	Kansas, Jefferson Co., Kansas River below Tecumseh, September, 1958.

Although neither *Carpiodes cyprinus* nor *Carpiodes forbesi* (see below) was mapped by Trautman (1956:Map 1) south of the Missouri River System, west of the Mississippi River, recent collections show it to be present in the Arkansas River System in Kansas (KU 8164 from Sedgwick Co. and KU 8241 from Sumner Co.) and possibly in the Colorado River System of Texas (OAM 5440 from the vicinity of San Angelo).

Variation and Zoogeography.—This carpsucker has, in several instances prior to the recent analysis of Bailey and Allum (1962:81) been recorded as *Carpiodes forbesi* Hubbs when mentioned from waters of the Great Plains. Bailey and Allum (1962:81) placed *C. forbesi* in the synonymy of *C. cyprinus,* noting that ". . . the slender fish with a low dorsal are likely the product of their environment." Although some environmental modification of the fish in the manner suggested by Bailey and Allum seems possible, the generally distinctive phenotype of *C. cyprinus* in the Great Plains probably is due in part to a different genetic heritage.

A fish resembling present-day plains populations of *C. cyrinus* may have originated in the Ancestral Plains Drainage. Subsequent to diversion of segments of the Ancestral Plains Drainage eastward, western populations may have mingled with closely related, but slightly different, congeners to the east. The result could reasonably be a wide zone of intergradation in the western Interior Lowlands, which might account for some of the difficulties in identifying specimens of this complex. Such a zone is suggested by the discernment of phenotypes of both "*cyprinus*" and "*forbesi*" in the Big Sioux River System in South Dakota and Iowa (Cleary, 1956, Maps 20 and 21; Bailey and Allum, 1962:81). Height of the dorsal fin in specimens from the Arkansas River System of Kansas varies to a degree that suggests a mosaic kind of intergradation.

Possibly western populations of *C. cyprinus* should be accorded subspecific status but until more specimens are available, allowing better insight into patterns of intergradation, this seems premature.

In any event the name "*forbesi*" is probably unavailable as the type locality in the Illinois River (Hubbs, 1930:13) was considered by Trautman (1956:39) as within the range of another subspecies—*Carpiodes cyprinus hinei* Trautman.

Carpiodes velifer (Rafinesque)

The high-finned carpsucker probably has been extirpated in the Kansas River Basin (Map 31); none is known to have been obtained since the 1920's. Records from the Basin were summarized by Minckley (1959:417-418). I have seen additional specimens (USNM 3549) attributed to the Republican River and collected by W. A. Hammond in the 1850's. Hay's (1887:247) record of "*Ictiobus velifer*" from Beloit, Kansas, probably is based on USNM 37936, which is instead *Carpiodes carpio carpio*. The pattern of extirpation for *C. velifer* resembles that for other species known to prefer the clearer waters seemingly more common prior to man's modifaction of the Kansas River Watershed.

Carpiodes carpio carpio (Rafinesque)

The river carpsucker is, by far, the most common of the deep-bodied suckers in the Kansas River Basin. It is found throughout the Basin from the larger waters of the east to shallow, sandy tributaries of the west (Map 32). It is rare in rubble-bottomed, upland creeks in the eastern part of the Basin. The western and southwestern inclination of the range of this species suggests an origin in the Ancestral Plains Stream and streams to the southwest, whence it penetrated eastward to a limited extent. The related species, *Carpiodes velifer*, on the other hand, might reasonably have originated in the Ancient Teays/Mississippi System.

Moxostoma erythrurum (Rafinesque)

Habitat and Distribution.—In the Kansas River Basin the golden redhorse has been taken only in Mill Creek, Wabaunsee County, Kansas (Map 33). It inhabits the larger pools of this clear, rubble-bottomed stream of the Flint Hills Uplands.

Zoogeography.—*M. erythrurum* is one of several fishes that are restricted to Mill Creek or to Mill Creek and a few nearby streams of the Flint Hills Area. The isolated occurrence of *M. erythrurum* is interpreted as relict; Mill Creek preserves habitat especially

favorable for fishes of clear upland streams. Elsewhere in the Missouri River System this species is presently found in Missouri in streams in or near the Ozark Uplift, in the Rock River, Iowa (Cleary, 1956: May 24) and in the lower Platte River in Nebraska (Larry A. Morris, unpublished master's dissertation, University of Missouri, 1960:28). Cope's (1871) types of "*Ptychostomus bucco*" from "St. Joseph, Missouri" (PAS 6961-64) are golden redhorse.

Moxostoma carinatum (Cope)

The only record of the river redhorse from the Kansas River System is based on an adult (KSU 2732) listed by Jennings (1942:364) as *Moxostoma aureolum* and reidentified by Frank B. Cross as *M. carinatum*. Jennings (1952:364) noted that the specimen was from the Wakarusa River, obtained by I. D. Graham, presumably in 1886 or a few years earlier.

Moxostoma macrolepidotum (LeSueur)

Habitat and Distribution.—The northern redhorse seems to inhabit most commonly the medium-sized streams of the eastern part of the Kansas River System (Map 34). In addition to the records presented by Minckley and Cross (1960) I have examined two specimens that provide the westernmost records from the basin, namely USNM 37930 (reported by Hay, 1887:247) from Beloit, Mitchell County, Kansas, in the Solomon River, and UMMZ 134994, obtained on July 8, 1940, by R. E. Johnson in the Little Blue River one mile southeast of Oak, Nuckolls County, Nebraska.

Zoogeography.—Minkley and Cross (1960) in assessing the taxonomic status of the northern redhorse in the Kansas River Basin considered specimens they examined to be intergrades between the subspecies *M. a. aureolum* (LeSueur) and *M. a. pisolabrum* Trautman and Martin. Hubbs and Lagler (1958:65) indicated that the name *aureolum* is unavailable in the genus *Moxostoma*. The name "*haydeni*" (*Teretulus haydeni* Girard) is available for populations of this species from the upper Missouri River according to Robins and Raney (1957:154), should these populations eventually be shown to differ subspecifically from the eastern *m. macrolepidotum*.

M. m. macrolepidotum is found in the upper Missouri River Basin and elsewhere to the north and east, whereas *M. m. pisolabrum* has its center of distribution in the Ozark Region. It seems, then, that

gene flow responsible for the element of *M. m. macrolepidotum* discerned in populations of the Kansas River Basin must have come from the north, and gene flow responsible for the element of *M. m. pisolabrum* from the southeast. A similar zone of intergradation between these subspecies was indicated for northeastern Missouri by Trautman and Martin (1951:8, Map 1). The present distribution of *M. m. macrolepidotum* (Trautman, 1957, Map 46; Minckley and Cross, 1960:35) over much of Canada indicates a fish tolerant of cold waters. *M. m. macrolepidotum* may have inhabited the upper Missouri System for a long period, perhaps in the preglacial Hudson Bay Drainage, and perhaps came into contact with *M. m. pisolabrum* only after deflection of the Missouri Drainage southward and eastward in one or more glacial advances. (It is not known whether the Missouri System after an initial deflection southward reacquired a northward direction of flow in any interglacial stage.) Either *M. m. macrolepidotum* endured the Wisconsinan glacial stage in the Upper Missouri Basin, or gained access to the Upper Missouri directly from the east through headwater connections with the Red or Minnesota rivers, such as were hypothesized by Bailey and Allum (1962:114) for some species inhabiting South Dakota. One of the above alternatives seems to apply because it is unlikely that *M. m. macrolepidotum* could, in postglacial time, have ascended the Missouri River System, passed genetically unaltered through the range of *M. m. pisolabrum* inhabiting the lower Basin, and then invaded and flourished in much of the upper Missouri River Basin.

Catostomus commersoni (Lacépède)

Habitat and Distribution.—The white sucker is found in smaller, clearer streams throughout much of the Kansas River Basin (Map 35). The distribution of this slender-bodied sucker complements that of the deeper-bodied sucker *Carpiodes carpio carpio.*

Variation and Zoogeography.—Evermann and Cox (1896:394) showed that *C. commersoni* in the Upper Missouri River Basin (Platte River northward) have larger scales, smaller eyes and more rows of papillae on the upper lip than do specimens from Ohio and Pennsylvania. They noted that the name *Catostomus sucklii* Girard is available for populations in the Upper Missouri Basin but added (p. 394), "We doubt, however, if *sucklii* should be recognized even as a subspecies . . ." Subsequently Ellis (1914:22-25) assigned white suckers from the Kansas River Basin in Colorado to *C. c.*

sucklii and Breukelman (1940:369), referring to suckers from the Kansas River Basin in northwestern Kansas, wrote, "The specimens we took are referable to subspecies *sucklii*, and the records probably apply to this form. Typical *commersonnii* is not known to occur farther west than the eastern third of Kansas, but the subspecies of this species have not been critically studied." Bailey and Allum (1962:85) did not partition *Catostomus commersoni* into subspecies.

My counts indicate (unpublished table 17 of doctoral dissertation by A. L. Metcalf, filed in Univ. Kansas Library, 1964) that white suckers from the Kansas, Arkansas, Canadian, and Pecos rivers are smaller-scaled than populations from the Platte System northward in the Great Plains. The mean number of lateral-line scales in specimens from these stream systems are as follows (listed east to west within system): Niobrara River, 59.6; western half of Platte River, 58.4, 59.7, 59.9; Marais des Cygnes River, Kansas, 67.5; Moniteau Creek, Missouri, 66.3; Kansas River, 65.3, 66.4, 65.8, 61.0; Arkansas River, Colorado, 63.8, 63.5, 62.7; Mora River, New Mexico, 65.6; Pecos River, New Mexico, 65.7. The mean of 61.0 from the Kansas River System was obtained from specimens taken below Enders Dam on Frenchman Creek in Hitchcock County, Nebraska. Introductions from the Platte River Drainage to the north may have taken place at this locality (see account of *Fundulus sciadicus*). Scale-counts in populations from the southern Great Plains closely resemble those from the lower Missouri River in Missouri and eastward in the Mississippi Valley.

Evermann and Cox (1896:393) noted that the number of dorsal rays in populations from the upper Missouri Basin is highly variable, but they stipulated no differences between these populations and those elsewhere. Bailey and Allum (1962:85) found that specimens from western South Dakota have slightly fewer dorsal rays than those from the eastern part of that state. I observed little difference in dorsal ray-counts of specimens from the Platte, Kansas, Arkansas and Pecos river systems, the number usually ranging from 11 to 13 with the average number approximately 12.

Evermann and Cox (1896:394) found, on the average, three or four rows of papillae on the upper lip of white suckers from the upper Missouri Basin and two or three rows on specimens from Ohio and Pennsylvania. (Rows of papillae are difficult to count because of their irregularity and the minuteness of some marginal papillae,

especially on small fish.) The average number of rows on specimens seen by me are as follows (series contain 7-20 specimens):

Ohio, Cuyahoga Co., Lake Erie Dr.	3.5
Wisconsin, Iowa Co., Fox River Dr.	3.7
Missouri, Moniteau Co., Moniteau Creek, Missouri River Dr.	3.4
Kansas, Riley Co., Kansas River Dr.	3.8
Kansas, Upper Smoky Hill River Dr.	4.2
Nebraska, Antelope Co., Verdigre Creek, Niobrara River Dr.	4.3
Wyoming, Platte Co., Laramie River	4.6
Colorado, Custer Co., Arkansas River Dr.	4.7
New Mexico, Mora Co., Mora River, Canadian River Dr.	4.5
New Mexico, San Miguel Co., Pecos Dr.	4.6

The number of rows of papillae increases westward and in this respect specimens from the Kansas River Basin are intermediate between those of the lower Missouri River Basin and those of western drainages such as the Arkansas, Pecos and upper Platte rivers. Specimens from the Smoky Hill River System resemble western populations.

Southwestern populations of *C. commersoni* in the Great Plains seem chubbier anteriorly, those from the Platte System northward more slender; but, 22 proportional measurements made on young fish 50-80 mm in standard length failed to reveal outstanding differences. Seemingly the differences become more pronounced in older fish.

Examination of a few series of white suckers suggests that Evermann and Cox (1896:394) rightly ascribed relative smallness of eye to populations from the Great Plains. Means obtained for distance across exposed surface of the eye expressed as thousandths of standard length were as follow: Wisconsin, Iowa Co., Fox River Drainage (KU 5379), 64.7; Kansas, Kansas River (Composite), 60.1; Nebraska, Garden Co., North Platte River (KU 4840), 58.8; Colorado, Weld Co., South Platte River (KU 4799), 56.6; New Mexico, San Miguel Co., Pecos River (KU 4268), 57.0.

In summary, there is a trend in the western part of the Mississippi River System towards a smaller eye and more papillose lips from east to west; towards smaller scales from north to south, and possibly towards a chubbier body-form from northeast to southwest. Perhaps these trends have zoogeographic significance. The Ancestral Plains Stream System probably was inhabited by *Catostomus commersoni* since (1) fossil remains of it have been reported from mid-Pleistocene (Illinoian?) beds of northwestern Oklahoma and

southwestern Kansas (C. L. Smith, 1954:283; 1958:177, 179, and G. R. Smith, 1963:281), and (2) the species still occurs in the western (Arkansas and Canadian rivers) and northern (Kansas River northward) parts of this hypothetical early drainage. It seems reasonable to suppose that the ancient Hudson Bay drainage also harbored *C. commersoni* because its present range extends far to the north in Canada and to high altitudes in the Rocky Mountains. If, as suggested by Greene (1935:59), this cold-tolerant fish followed glacial fronts northward in association with coregonids and salmonids it may have inhabited the northern part of the Great Plains (Dakotas, Montana, and Wyoming) throughout much or all of the Pleistocene. The widespread occurrence of this species in the eastern United States, including some Atlantic coastal drainages, strongly suggests that it also inhabited the preglacial Teays/Mississippi System.

If three geographically-separated representatives formerly existed, the representative of the Ancestral Plains Stream Drainage may have been a chubby fish with many lip-papillae, and small eyes and scales. Fish from the western part of the Hudson Bay Drainage may have resembled the representative from the Plains except for slenderer body and larger scales. Populations from the Teays/Mississippi may have possessed a large eye, slender body, small scales, and lips with few papillae. Assuming that such distinctiveness did exist, it has been blurred subsequently in the Mississippi River System by Pleistocene mingling of stocks caused by advances of glacial ice, compression of ranges and changes in stream connections. Such blurring seems especially detectable in the Kansas River Basin, which is occupied by a fish most nearly resembling populations of the Missouri/Mississippi System to the east but sharing a few characters with populations to the north and southwest.

Ictalurus punctatus (Rafinesque)

The channel catfish is widespread in the Kansas River Basin (Map 36) and has long inhabited streams of the Great Plains as shown by Pliocene and Pleistocene fossil remains (C. L. Smith, 1954:285; 1958:179; 1962:507 and G. R. Smith, 1963:281). Like several other catfishes of the Mississippi Basin, *I. punctatus* is tolerant of large, turbid rivers, readily disperses therein, and therefore is of little significance in elucidating zoogeographic patterns.

Ictalurus furcatus (LeSueur)

The only specimen of blue catfish that I have examined from the Kansas River Basin is KU 7488 (head only) taken in the Kansas River at Lawrence, Douglas County, Kansas, in July, 1942. Both Snow (1875:141) and Dyche (1914:76) wrote of large blue catfish taken at Lawrence. The species is known from the Missouri River as far upstream as Iowa (Harlan and Speaker, 1956:108) and South Dakota (Bailey and Allum, 1962:90).

Ictalurus natalis (LeSueur)

Habitat and Distribution.—The yellow bullhead is common in small streams of the Basin from the Flint Hills eastward (Map 37). Minckley (1959:427) observed it to inhabit the mud-bottomed streams and upland, gravelly creeks, of the Big Blue River System in Kansas.

Westward from the Flint Hills this species is rare in collections. Early collectors failed to record it from the western part of the Basin. Possibly its occurrence there in more recent years (first recorded from the Saline River by Breukelman, 1940:372) is due to introduction by man. Peripheral records in addition to those of Breukelman are as follows: KU 7203—Smoky Hill River, 2.5 mi. SW Wallace, Wallace Co., Kansas, August 24, 1961 (12); KU 7011—Foster Creek, 5.5 mi. NW Orleans, Harlan Co., Nebraska, July 18, 1961 (5); KU 4051—Sappa Creek, Decatur Co., Kansas, sec. 29, T. 2 S, R. 28 W, June 23, 1958 (1).

Zoogeography.—Ictalurus natalis is widespread in the eastern United States (Hubbs and Lagler, 1958:90; Trautman, 1957: Map 106). Populations in the Kansas River System are on the northwestern periphery of the range of the species and probably entered the Basin from the southeast.

Ictalurus melas (Rafinesque)

Habitat and Distribution.—The black bullhead is the commonest of the catfishes inhabiting the Kansas River Basin (Map 38). It seems to tolerate a wide variety of habitats, although its distribution is somewhat complementary to that of the larger catfishes, *Ictalurus punctatus* and *Plyodictis olivaris*—the latter species being more common in the larger streams of the Basin. *I. melas* and *Pimephales promelas* seem to be the only species that presently

thrive in the highly turbid, mud-bottomed, low gradient streams of the upper Big Blue River in Nebraska (Lincoln Creek, Beaver Creek and North Fork Big Blue River).

Variation and Zoogeography.—Northern (*I. m. melas*) and southern (*I. m. catulus*) subspecies have been recognized by some workers (Ortenburger and Hubbs, 1926:134; Hubbs and Ortenburger, 1929a:39; Hubbs and Lagler, 1958:90) but not by others (Trautman, 1957:427; Bailey, 1956:328; Bailey and Allum, 1962:88). Hubbs (1940b:209-210; 1945:19) noted that northern populations possess a heavier body, smaller spines and shorter anal fin than southern representatives. Anal fin-rays in *I. m. catulus* have been enumerated as 19-23 (Ortenburger and Hubbs, 1926:134); for *I. m. melas* as 17-21 (Hubbs and Lagler, 1958:89). The number of anal rays in specimens examined by me from the Kansas River System seems to be intermediate between that of specimens from the Arkansas River System and some from tributaries of the Missouri River north of the Kansas River in Kansas. Means and ranges for 13 specimens from the area last named are 19.2 (18-20); for 37 specimens from the Kansas River System 20.9 (19-24) and for 20 specimens from the Arkansas River in Kansas 22.0 (21-24). The average number of anal rays in specimens from the eastern part of the Kansas River Basin is 20.8 and in 9 specimens from Hackberry Creek in the Smoky Hill Drainage is 21.2.

Fossils (C. L. Smith, 1945:285; 1958:178 and G. R. Smith, 1963: 281) show that *I. melas* occupied a part of the Great Plains in southwestern Kansas and northwestern Oklahoma in the Middle Pleistocene (Illinoian?). This fact and the ubiquity of the species in the Great Plains at present, suggest that it inhabited the Ancestral Plains Stream Drainage. Possibly the species inhabited also the Hudson Bay Drainage. Initial separation with subsequent mingling of faunas from these two drainages may have given rise to a situation in which slightly different kinds inhabit northern and southwestern segments of the western part of the Mississippi River System; these kinds are connected by a wide zone of intergrading populations.

Ictalurus nebulosus (LeSueur)

Cragin (1885b:107) listed the brown bullhead from "Various streams about Topeka. Also Lawrence (Snow) and Ottawa (Wheeler)." Graham listed it (1885a:71) as "Plentiful" in Kansas

and specified (1885b) its presence in the Kansas River. The "bullheads" seem to have been confused by workers of the last century. Later workers have failed to find this species in the Kansas River Basin. However, in recent years it has been introduced into farm ponds in the Basin.

Noturus flavus Rafinesque

Habitat and Distribution.—Records of the stonecat are scattered throughout much of the Kansas River Basin (Map 39). There are both older (1800's) and more recent records from most parts of the Basin, indicating that *N. flavus* is native to the Basin and that it has withstood modifications of stream-habitats that seem to have taken place.

Noturus flavus occurs in streams with either sandy or rubbly bottoms. As pointed out by Minckley (1959:428), *N. flavus* occurs in the Blue River along sand flats where no rubble cover is available. In nearby rubbly riffle-habitats of Flint Hills streams (Camp Creek in Pottawatomie County and Clark Creek in Morris County) I found large concentrations of this species in April, 1962. In the western part of the Basin the stonecat was usually found under large flat stones that occasionally strewed the predominantly sandy streambeds.

Zoogeography.—*Noturus flavus* is widespread in the upper Mississippi River Valley (Hubbs and Lagler, 1958:90) including most parts of the Missouri River System. As suggested by Bailey and Allum (1962:121) it is one of a large number of species that could employ the Missouri River mainstream as an avenue of dispersal.

Noturus exilis Nelson

Habitat and Distribution.—The slender madtom has a restricted distribution in the Kansas River Basin (Map 40), having been taken only in the Mill Creek System in Wabaunsee County, Kansas (KU 4672, KU 8117) and in Washington Creek, a tributary of the Wakarusa River, Douglas County, Kansas (KU 4675). In these streams it is restricted to riffle habitats of the headwater creeks typical of the uplands of the Flint Hills and Shawnee Escarpments. In the Mill Creek System it has been taken at numerous stations in headwater tributaries. In Washington Creek, however, it has been found only in a short section of permanently-flowing stream downstream from Lone Star Lake, an impoundment of approximately

200 acres completed in 1939. No specimens were taken in the lowermost, mud-bottomed sections of either Mill Creek or Washington Creek.

Zoogeography.—Noturus exilis is a representative in the Kansas River Basin of a clear-water fauna of Ozarkian affinities. Probably it entered the Basin from the east at a time when streams were less inimical to it than at present. West of the Osage River in the Missouri River System it has persisted only in favorable habitat, as in the streams noted above and in Moniteau Creek, Moniteau County, Missouri (KU 6477), Moreau Creek, Morgan County, Missouri (KU 6470), and Indian Creek, a tributary of Blue River (entering the Missouri River in Jackson County, Missouri), Johnson County, Kansas (KU 4335).

Pylodictis olivaris (Rafinesque)

The biology of the flat-headed catfish in Kansas, including the Big Blue River System, was studied by Minckley and Deacon (1959). They noted that in Kansas this species is present in major rivers and impoundments and usually is absent from intermittent streams (Map 41). *P. olivaris* has been reported as far west as Gove County, Kansas (KU 2073, from Hackberry Creek). It is of little significance zoogeographically here, because it is widespread in larger streams of the Mississippi River Basin and some other Gulf drainages (Moore, 1957:142).

Anguilla rostrata (LeSueur)

In recent years the American eel has been taken only in the lower part of the Kansas River Mainstream (Map 42). Formerly, as indicated by Breukelman (1940:372), this species was found upstream as far as Big Creek (probably in Ellis County, Kansas) and possibly to Beaver Creek in Rawlins County, Kansas.

Fundulus kansae Garman

Habitat and Distribution.—The plains killifish seems pre-eminently adapted to life in shallow, sandy streams of the Great Plains. It reverses the distributional pattern exhibited by most fishes of the Kansas River Basin in that it is most abundant in the western rather than in the eastern half of the Basin (Map 43). Eastward it seems to be restricted to the mainstream of the Kansas River. To the

northeast, *Fundulus kansae* has been recorded in Clay and Howard counties, Missouri (Miller, 1955:11) and from the Nemaha River Drainage of southeastern Nebraska (KU 7152, 8 mi. south of Syracuse in Muddy Creek). In the Missouri River mainstream it has been taken as far downstream as New Haven, Franklin Co., Missouri (Fisher, 1962:428).

Zoogeography.—Fundulus kansae probably originated in the Ancient Plains Stream. Its present range coincides well with the supposed limits of such a stream system (Fig. 3). To the east a few records are known beyond such limits (see above) possibly representing stragglers from the west. To the north this species is thought to have occurred naturally only as far as the Platte or Niobrara systems (Miller, 1955: 11, 12). Recent records in South Dakota are interpreted by Miller (1955) as introductions by man. Introductions may account also for the presence of the species in the Big Horn River in Wyoming (KU 6869, taken by Charles A. Long on June 22, 1961, one mile west of Greybull).

To the south either *F. kansae* or *F. zebrinus* Jordan and Gilbert (a possibly distinct, but closely related species) has been reported from the Arkansas, Red, Brazos, Colorado and Pecos drainages. This distributional pattern suggests some interchange of faunal elements of these streams in the past. The incorporation of parts of the Platte, Kansas and Arkansas rivers into the Ancient Plains Stream has been described elsewhere and the possible inclusion of, or interchange with, parts of the Red, Brazos and Colorado rivers has been suggested. Koster (1957:1) postulated a connection of the Upper Canadian and Upper Pecos systems in New Mexico.

Fundulus sciadicus Cope

Habitat and Distribution.—To my knowledge the only records of the plains topminnow from the Kansas River Basin are provided by Cope (1865:78, 85) and by a series (KU 4856) taken below Enders Reservoir, Hitchcock County, Nebraska, on September 11, 1959. In his original description Cope lists the species "from the Nebraska or Platte River," whereas later in the same paper he includes it in a list of fishes "from the Platte River, near Fort Riley." Cope's material probably came from the Platte Drainage where the species occurs naturally. R. E. Johnson (unpublished dissertation, University of Michigan, 1942) in his intensive survey of the waters of Nebraska did not find *F. sciadicus* in the Kansas River

System in that state. I suspect, therefore, that the species has been introduced into the Republican River Drainage, adjacent to the Platte, in recent years. Several reservoirs, intensively fished, are located in the upper Republican Drainage.

In addition to its occurrence in the Platte River to the north, *F. sciadicus* is found in some tributaries of the Missouri River downstream from the Kansas River in central Missouri (KU 6451, 6454, 6494).

Probably the species was formerly more widespread in the Great Plains. Bailey and Allum (1962:93) noted that it "was formerly rather common in clear creeks in southern South Dakota, but appears now to be uncommon." Bailey (1956:157) suggested that it might be on its way to extinction in Iowa. In Nebraska it occurs more widely but this may be due, as suggested above, to artificial transplanting. I have collected *F. sciadicus* (KU 7116) in association with *Chrosomus eos* (KU 7118) and *Chrosomus neogaeus* (KU 7119) in the sandhills region of Nebraska. The *Chrosomus* spp. occurring in this region have been considered relicts (Hubbs and Lagler, 1958:80; Bailey and Allum, 1962:40-42).

Zoogeography.—Zoogeographically *F. sciadicus* is puzzling. Its restriction to waters west of the Mississippi strongly suggests an origin in the Ancient Plains or Ancestral north-flowing Missouri drainages. However, its current absence over much of the area thought to have been drained by these systems is hard to explain, other than by widespread extirpation. Its occurrence in tributaries of the Neosho River System in southeastern Kansas, southwestern Missouri and northeastern Oklahoma is also puzzling. These populations may be (1) relicts of the fauna of the Ancestral Plains Stream (this stream-system may have included parts of the ancestral Neosho drainage—see Quinn, 1958:41, 42, Fig. 1), or (2) due to headwater-transfer to the Neosho River Drainage (Spring River) from southern tributaries of the Missouri River.

Lota lota (Linnaeus)

From the Kansas River I have seen only one specimen (KU 7487) of the burbot. It bears the data "Kaw River, Lawrence, Kansas, 1906." Gilbert (1886:210) reported the burbot from the Missouri River at Leavenworth, Kansas, and Fisher (1962:428) took one specimen at St. Joseph, Missouri. An additional specimen from the Missouri River is KU 3162, taken eight miles south of Atchison,

Kansas, on April 3, 1953. Occurrence of the burbot in this part of the Missouri River not far from the mouth of the Kansas River suggests that the species may still enter the lowermost mainstream on occasion.

Lota lota, a holarctic species widespread in Canada and northern United States, might have gained access to the Missouri River Basin either from the north (preglacial Missouri) or the east or from both directions.

Roccus chrysops (Rafinesque)

The white bass is most abundant in (1) the lower Kansas River Mainstream, (2) impoundments of the Basin, and (3) streams near such impoundments (Map 44). Minckley (1959:428) assumed that the white bass was indigenous to Kansas on the basis of reports of Cragin (1885b:111) and Graham (1885a:77; 1885b). Cragin attributed *R. chrysops* to Mill Creek in Shawnee Co., Kansas and to Eureka Lake (Eureka Lake was an oxbow lake along the Kansas River immediately west of Manhattan, Riley County, Kansas). From this same area Minckley (1959:428) recorded *R. chrysops* caught in 1957 and 1958. Snow (1875:140) reported "*Labrax chrysops*" from the Kansas River at Lawrence. I found young white bass to be common in the Kansas River at Lawrence and at Eudora, Kansas, in the summer of 1961.

Micropterus dolomieui Lacépède
and
Micropterus punctulatus Rafinesque

According to Mr. Roy Schoonover, Chief, Fisheries Division, Kansas Forestry, Fish and Game Commission (personal communication) a few small-mouthed bass and spotted bass have been planted in Cedar Bluff Reservoir, Trego County, Kansas.

Micropterus salmoides salmoides (Lacépède)

Records for the large-mouthed bass are scattered through much of the Kansas River Basin. Probably it is native in the Basin as Graham (1885a:76) wrote that it was "Reported from branches of Kansas river, below dam at Lawrence." Cragin (1885b:110) listed the species from Soldier Creek, Shawnee Co., Kansas, and Dyche (1914:45) wrote "The Black bass is one of the original native

Kansas fishes, and at one time, in the early history of the country when settlements were few and far between, it was rather common in the smaller and the middle-sized streams of the state." In addition this species of bass has been widely stocked in farm-ponds and other impoundments in Kansas (Minckley, 1959:429; Hastings and Cross, 1962:15).

Chaenobryttus gulosus (Cuvier)

I have seen no specimens of the warmouth from the Kansas River Basin other than those from impoundments. However, Graham (1885a:75) listed the warmouth from the Kansas River, which suggests that the species may have occurred natively in streams of the Basin.

Lepomis cyanellus Rafinesque

Habitat and Distribution.—The green sunfish occurs widely in the Kansas River Basin, both in streams and impoundments (Map 45). It is most abundant in lentic situations.

Zoogeography.—Branson and Moore (1962:90, 91) presented evidence indicating that *L. cyanellus* may be the most primitive member of its genus. That the species is a venerable one receives substantiation from C. L. Smith's (1962:516) report of fossil material of late Pliocene age referable to this species. C. L. Smith (1954: 286; 1958:179) and G. R. Smith (1963:282) also found material of Pleistocene (Illinoian?) age resembling *L. cyanellus* in southwestern Kansas and northwestern Oklahoma. Clearly, then, *L. cyanellus* or its progenitors occupied the Great Plains at least since Late Pliocene time, suggesting adaptibility to, and tolerance of, conditions of this region. Its tolerance of adverse conditions such as oxygen depletion, stagnation and partial desiccation of creeks and ponds was pointed out by Gerking (1945:99), Lewis and Dalquest (1957:46) and Metcalf (1959:392).

The absence of *L. cyanellus* from Atlantic coastal drainages (Trautman, Map 133) suggests that its origin has been western or southwestern. From such a center it seems to have penetrated as far east in drainages of the Gulf Coast as the Alabama River and possibly the Escambia River (Bailey, Winn and Smith, 1954: 137) and up the Mississippi Valley where habitat is favorable to it. That this habitat is suggestive of Plains conditions is indicated by Forbes and Richardson (1909:249), who wrote that the green

sunfish was "almost the sole sunfish product of the net in the prairie creeks." In Ohio Trautman (1957:501) found it in streams having low or moderate gradient and noted its tolerance of turbidity and siltation.

Lepomis megalotis (Rafinesque)

The long-eared sunfish is rare in the Kansas River Basin (Map 46). I have examined only four collections: (1) KU 1953—Rock Creek (tributary of Wakarusa River), Douglas County, Kansas, August 11, 1951 (1 specimen), (2) KU 6743—this and the two succeeding lots are from the Mill Creek Drainage, Wabaunsee County, Kansas. August 9, 1953 (2 specimens), (3) KU 7446—July 25, 1963 (10 specimens) and (4) KU 8116—May 9, 1964 (14 specimens). The species has been taken in the Mill Creek System on other occasions. The record of Minckley (1956:353) from Deep Creek, Riley County, Kansas, is probably invalid, as it was based on a field identification made by me that I suspect was in error.

In the absence of early records it is not entirely clear that this species is native to the Basin. However, its association with other members of the "Mill Creek Fauna" (discussed elsewhere) that have eastern affinities suggests that it reached the Basin from the east at a time when streams may have been clearer, and has persisted only in the habitat most favorable to it in the Flint Hills and Shawnee Escarpments.

Specimens from the Kansas River System possess a red predorsum (unpigmented in alcoholic specimens).

Lepomis humilis (Girard)

Habitat and Distribution.—The orange-spotted sunfish occurs widely in the Kansas River System (Map 47). It is almost as common as the green sunfish; the two are often taken at the same stations. Like that species it is most common in pools where aquatic vegetation provides some cover. In Deep Creek, Riley County, Kansas, Minckley (1956:355) found *L. humilis* "in water less than four feet deep, and in or near loose rock, algae, brush, or other cover."

Zoogeography.—Like *Lepomis cyanellus, L. humilis* is primarily a Plains fish. Branson and Moore (1962:93) noted that "Its range indicates a preference for turbid waters . . ." Where it occurs outside the Great Plains, *L. humilis* seems to choose (or is relegated by competition to) stream-habitats most nearly resembling those

of the Plains. In some instances a correlation between increase of such habitat in connection with agricultural modification of the watershed and the extension of range of *L. humilis* has been suggested. Thus, in Illinois, Forbes and Richardson (1909:256) found *L. humilis* to be most abundant in the prairie region of that state. Gerking (1945:101) found it much more abundant in silty, than in clear, streams, in Indiana. In Ohio, Trautman (1957:506-508) documented the invasion of this species from the west into the central part of the state. He correlated this invasion with an increase in stream-turbidity and increased siltation of stream bottoms.

Possibly *L. humilis* had its origin in the Ancestral Plains Stream System. From this postulated center it has made modest invasions to the southeast in Gulf Coastal drainages as far as the Pearl River (according to Cook, 1959:182) and northeastward as noted above.

Lepomis macrochirus Rafinesque

The bluegill has been stocked in farm ponds (Hastings and Cross, 1962:15) and other impoundments in the Kansas River Basin. Its ubiquity and tolerance of a wide variety of habitats in the Basin suggest that it may be native, as does the allusion to this species by Graham (1885a:76) and possibly by Snow (1875: 140—as *Pomotis luna* Girard).

Ambloplites rupestris (Rafinesque)

The record of Snow (1875:140) seems to be the only evidence that the rock bass occurred natively in the Kansas River Basin. However, Snow did not list *Lepomis cyanellus* from the Kansas River at Lawrence, a species that would have been expected there; possibly Snow confused these two species. The rock bass is found eastward in the Missouri River Drainage in the Ozark Region and may formerly have existed farther west.

I have examined one specimen (UMMZ 134355) taken from a small creek below a fish hatchery 1½ miles east of Benkelman, Dundy County, Nebraska, on July 24, 1939, by R. E. Johnson. This record is almost surely the result of introduction by man.

Pomoxis annularis Rafinesque

The white crappie has been taken at scattered localities throughout most of the Kansas River Basin. Several older records (Snow, 1875:140—as *Pomoxys hexacanthus;* Graham, 1885a:75; Cragin,

1885b:110; Jennings, 1942:366) probably are referable to this species, and the statements of Dyche (1914:54-57) noted below strongly indicate that this species is native to the Basin. Dyche wrote (p. 54), "The Crappie is a native Kansas fish. As early as 1867, '68, '69 and '70, the writer caught strings of them in the Wakarusa river and its tributaries. In 1871 and '72 he took them in Mill creek, Mission creek . . ." and (p. 56), "The crappies that the author caught in Kansas some forty years ago were, as he remembers them, of the white variety. All specimens collected some thirty years ago and preserved for the State University Museum are of the light-colored or white species." In addition the white crappie was planted early in the waters of Kansas according to Graham (1885a:78) and in Nebraska, South Dakota and Kansas according to Evermann and Cox (1896:417).

Pomoxis nigromaculatus (LeSueur)

Records of the black crappie are scattered through much of the Kansas River Basin. It is not so abundant nor so widespread as the white crappie. That the black crappie, unlike the white crappie, may be an introduced species is suggested by the lack of older records, by Dyche's remarks noted above under the account of *P. annularis*, and by his statement (1914:57): "The first Black crappies that the author remembers having seen in Kansas were taken at Lake View, being propagated from stock that the United States Fish Commission car planted there nearly twenty years ago." (Lake View is an oxbow lake in Douglas County west of Lawrence.) Graham (1885a) did not list this fish in the fauna of Kansas nor did Cragin (1885b:110) list it in the Kansas River.

Stizostedion vitreum vitreum (Mitchill)

The walleye was, according to Graham (1885a:78), stocked in the waters of Kansas by the 1880's. In recent years it has been stocked in several reservoirs in the Basin.

There is also some indication (Cragin, 1885b:11; Graham, 1885a: 77, 1885b) that the species was native to the Basin. Three specimens (USNM 31464) in the National Collection, catalogued in 1882, bear the following data: "*Stizostedium vitreum* var. *salmoneum*. Valley Falls, Kansas, July 7, J. L. Whitman." The fish are in a good state of preservation. Characters are as follows: soft dorsal rays: 21, 21, 22; pyloric caeca: 4, unknown, 3; black spot at

posterior end of spinous dorsal fin in all; cheeks sparsely scaled in all. *S. v. vitreum* is wide-ranging, seemingly highly vagile, and difficult to appraise zoogeographically.

Stizostedion canadense (Smith)

The sauger was recorded from the eastern part of the Kansas River Basin by several early workers (Cragin, 1885b:111; Graham, 1885a:77, 1885b; and possibly by Snow, 1875:140, as *Lucioperca americana*). Specimens are still taken occasionally below Bowersock Dam in the Kansas River at Lawrence.

Perca flavescens (Mitchill)

The yellow perch is not known to have been native to the Kansas River Basin but it has been introduced into several impoundments.

According to Gile (1885), Graham (1885a:78) and Cragin (1885b:111) this species was brought into Kansas in the 1800's. Ellis (1914:105) noted that *P. flavescens* had been introduced into Colorado, Montana and the Pacific States, listing several specimens from Colorado, some taken as early as 1900. Simon (1946:98) mentioned introduction of this species into Wyoming waters.

Bailey and Allum (1962:102) suggested that *P. flavescens* gained access to the middle Missouri River System in post-glacial time. However, the records of C. L. Smith (1954:286; 1958:178) and G. R. Smith (1963:283) of fossil material referred to this or a closely related kind from beds of Pleistocene age in southwestern Kansas and northwestern Oklahoma indicate that it ranged far to the south in the Great Plains in Illinoian (?) time. That subsequently it was extirpated in the western Plains suggests occurrence of a period or periods of marked aridity there, possibly in Sangamonian or in post-glacial time.

Percina caprodes (Rafinesque)

The logperch has been taken only in the Flint Hills and Shawnee Escarpments, in upland creeks with clear water and bottoms predominantly of rubble and gravel (Map 48). The westernmost specimens that I have seen are from Riley County, Kansas (UMMZ 122045, collected by Minna Jewell in September, 1923, from Deep Creek; KSU 3401, 3417, and 2999, taken in the 1880's from Wildcat Creek and KSU 25167, taken in 1958 from Eureka Lake, an oxbow two miles west of Manhattan).

The logperch inhabits clear waters typically occupied by Kansas River fishes having Ozarkian affinities. Logperch from the Kansas River System have been called *P. c. carbonaria,* a subspecies not known upstream from the Kansas River in the Missouri River Basin; another subspecies, *P. c. semifasciata,* is reported from eastern South Dakota by Bailey and Allum (1962:104). It is logical to suppose that Kansas River populations were derived from the southeast (probably from the Ozarkian Region). *P. c. carbonaria* is widespread in the lower Mississippi Valley and some drainages of the Gulf Coast (Bailey, Winn, and Smith, 1954:141; Cook, 1958:195).

Percina maculata (Girard)

To my knowledge, the first specimens of the black-sided darter to be found in the Kansas River Basin in almost 70 years were recently taken in the Mill Creek Drainage, Wabaunsee County, Kansas as follows: (1) KU 7447—sec. 11, T. 12 S, R. 10 E, taken on July 29, 1963, by Bill Cole and Verlyn Evert and (2) KU 8122—sec. 15, T. 12 S, R. 10 E, taken on May 9, 1964 by Frank B. Cross. Each of the collections contained only one specimen. There are, however, earlier records for this species. Gilbert wrote (1886:209) "*Hadropterus aspro* Cope and Jord.—Numerous specimens from Snokomo Cr., Wabaunsee Co. (Myers), this being its first definite record from Kansas." Jennings (1942:365) listed a specimen in the Museum of Kansas State University, Manhattan, taken in Wildcat Creek, Riley County, Kansas, in 1894. The record of Jennings probably refers to KSU 2884, a faded specimen collected in September, 1894 from Wildcat Creek, that I have examined and found to be *P. maculata.* Two additional specimens (KSU 2742) with no data other than "I. D. Graham" are also extant in the collections of Kansas State University.

The black-sided darter is one of a number of species that seems to have suffered restriction of range in the Kansas River Basin. The species has been reported from localities both downstream and upstream from the mouth of the Kansas River in the Missouri River System. Perhaps it penetrated westward into the Kansas River Basin at a time when streams offered habitat more favorable to it than at present. This may have occurred during that time in the Pleistocene when the eastern part of the Kansas River headed east of or in the Flint Hills.

Etheostoma nigrum nigrum Rafinesque

Early collections indicate that the johnny darter was widespread in small streams over much of the Kansas River Basin. Currently it is mainly restricted to some of the most favorable small-stream-habitat in the Flint Hills and Shawnee Escarpments (Map 49). Hay (1887:243, 249, 250) and Gilbert (1889:39) reported johnny darters from several western localities. I have been able to check the identity of Hay's specimens (three in number) from Beloit (USNM 37964). An isolated record from the Blue River System of Nebraska consists of one specimen (UMMZ 135368) taken by R. E. Johnson on the West Fork of the Big Blue River, three miles east of Stockham, Hamilton County, Nebraska, on July 7, 1940.

The Kansas River Basin is on the western periphery of the range of this widespread species; it seems to have entered the Basin from the east.

Etheostoma spectabile pulchellum Girard

Habitat and Distribution.—The orange-throated darter is found in most parts of the Kansas River Basin (Map 50). It generally avoids the siltier streams, in the area mantled by glacial till and in the central and western parts of the Basin where agriculture is intensive. It is, therefore, an indicator-species of the better waters of the Basin and its extirpation from a stream is a sign of worsening conditions (Deacon and Metcalf, 1961:320).

Zoogeography.—Variation and systematics of this species are being studied by Mr. Donald A. Distler, University of Kansas. Most populations in the Kansas River Basin appertain to the subspecies *E. s. pulchellum,* although there is (Distler, personal communication) progressive intergradation eastward in the Basin with the typical, eastern subspecies. The subspecies *E. s. pulchellum* inhabits the Great Plains from the Platte River Drainage southward into Texas. Probably this kind was dispersed by a common drainage such as was provided by the Ancestral Plains Stream System.

Aplodinotus grunniens Rafinesque

The freshwater drum inhabits the larger streams and reservoirs, especially in the eastern part of the Kansas River Basin (Map 51). Westward the species becomes scarce. Judging from the localities represented (Map 51) this is one of many species of fishes that find large turbid rivers no barrier to dispersal in the Basin.

SPECIES PROBABLY OCCURRING IN THE KANSAS RIVER BASIN

These species have been reported in the literature, but supporting specimens are unknown:

Acipenser fulvescens Rafinesque.—Snow (1875:140) reported "*Acipenser maculosus*" from the Kansas River, noting that the largest specimen taken weighed 26 pounds. Cragin (1885b:106) and Graham (1858a:70) listed "*Acipenser rubicundus*" from the Kansas River, Cragin indicating that this was on authority of Snow. Harlan and Speaker (1956:47) found the lake sturgeon to be confined to the Mississippi River in Iowa. Bailey and Allum (1962: 108) failed to find the species in the Missouri River Drainage in South Dakota. They suggested that reports of large sturgeon from the upper Missouri River Drainage might be attributable to *Scaphirhynchus albus,* which is known to attain a large size. Bailey and Allum also stated (p. 108) "We know of no verified record of the lake sturgeon in the Missouri basin above the mouth of the Kansas River (Johnson, MS)." However, Johnson (unpublished dissertation, University of Michigan, 1942) recorded specimens of *A. fulvescens* from the lower Platte and Elkhorn rivers in Nebraska. I know of no verifiable records from the Kansas River Basin.

Amia calva Linnaeus.—Evidence is meager that the bowfin is native to the Kansas River Basin; indeed, Bailey and Allum (1962: 30) doubted its occurrence anywhere in the Missouri River Basin. Subsequently, Fisher (1962:427) listed it from the lowermost part of the Missouri River. There is a record by Cope (1865:86) from "Platte River, near Fort Riley," based on collections of the expedition of Lt. F. T. Bryan, discussed elsewhere. Graham (1885a:71) listed this fish from "Branches of Missouri River" in Kansas.

Alosa chrysochloris (Rafinesque).—There is little evidence that the skipjack herring ever occurred in the Kansas River System. Graham (1885a:77) listed it as abundant in the larger streams of Kansas; however, Graham did not list *Dorosoma cepedianum,* a species now abundant in these streams. I suspect that Graham confused the two species. Evermann and Cox (1896:413) listed no records from the Missouri River Basin other than those of Graham. Forbes and Richardson (1909:49) noted that *A. chrysochloris* occurred in the "larger streams of Kansas"; possibly this information was also obtained from Graham. Harlan and Speaker (1956:59) did not find *A. chrysochloris* in the Missouri River

Drainage in Iowa, nor did Fisher (1962) list it from the lower Missouri River. However, Bailey and Allum (1962:31) reported one specimen from Fort Randall Dam on the Missouri River in South Dakota.

Hiodon tergisus LeSueur.—The mooneye has been listed from Kansas by Cope (1865:85, "Fort Riley"), Graham (1885a:74; 1885b), Cragin (1885b:109, "Kansas R. at Topeka"), and Evermann and Cox (1896:413). Bailey and Allum (1962:108) did not find any evidence justifying its inclusion in the faunal list of the upper Missouri River nor did Harlan and Speaker (1956:61) record it from the Missouri River Drainage of Iowa. However, Fisher (1962: 427) listed it from several stations on the lower part of the Missouri River, as far upstream as Atchison County in northwestern Missouri, and Johnson (unpublished dissertation, University of Michigan, 1942) reported one specimen from the lower Platte River in Nebraska.

Notropis hudsonius hudsonius (Clinton).—The spot-tailed shiner was listed by Cragin (1885b:108) and Graham (1885b) from Wildcat Creek (Riley County, Kansas) and by Graham (1885a:73) from "Kansas River Branches." A specimen (KSU 2835) bearing the data "I. D. Graham, 1886" is extant in the collections of Kansas State University. This species is native to the Missouri River Basin in eastern South Dakota (Evermann and Cox, 1896:404, Bailey and Allum, 1962:62), northwestern Iowa (Cleary, 1956: Map 45) and southwestern Minnesota (Underhill, 1957:17, Map 16). Formerly it may have occurred farther south in the Basin. This seems almost certain to have been the case during glacial stages of the Pleistocene.

Hypentelium nigricans (LeSueur).—Graham (1885a:72) listed the northern hog sucker from the Neosho and Kansas rivers. The species still occurs in the Neosho Drainage of Kansas. Possibly Graham erroneously ascribed specimens from that drainage to the Kansas River. However, *H. nigricans* occurrs in the Missouri River System as near to Kansas as Richland Creek, Morgan County, Missouri (KU 6889) and in the Osage River Drainage; it might formerly have ranged farther upstream. A specimen (KSU 2978) collected by I. D. Graham in 1886, but without further data, is preserved in the collections of Kansas State University.

Percopsis omiscomaycus (Walbaum).—Recognition of the trout-perch in the fauna of the Kansas River Basin rests on Gill's (1864: 151) description of "*Percopsis hammondi*" based on a specimen

supposed to have been taken in Kansas by W. A. Hammond. Gill's account seems to be responsible for subsequent inclusion of the trout-perch in the ichthyofauna of Kansas (Cope, 1865:85; Graham, 1885a:75; Cragin, 1885b:109; Forbes and Richardson, 1909:226; Eddy and Surber, 1947:197; Moore, 1957:160 and Bailey and Allum, 1962:94). If the specimen was actually obtained by W. A. Hammond it is likely, as pointed out elsewhere, that it came from the Kansas or Platte river systems.

Whether or not Gill's specimens actually were from the Kansas River Basin it is reasonable to suppose that *P. omiscomaycus* inhabited the basin in historic time or in conjunction with glacial advances. Some other fishes with the northern affinities exhibited by *P. omiscomaycus* were shown by C. L. Smith (1954, 1958) to have existed even farther south than the present Kansas River Basin in Illinoian (?) time. Furthermore, *P. omiscomaycus* ranges not far from the Kansas River Watershed even now, having been recorded in southwestern Iowa (Cleary, 1956: Map 71) and north-central Missouri (Hanson and Campbell, 1963:139).

Etheostoma blennioides Rafinesque.—The sole record of the green-sided darter in the Kansas River Basin is that of Graham (1885a:76; 1885b) from Wildcat Creek, Riley County, Kansas (repeated by Cragin, 1885b:110). One specimen (KSU 2885), bearing only the data "I. D. Graham," is extant in the collections of Kansas State University. In regard to certain scale-counts (59 in lateral line and 19 around caudal peduncle) this specimen shows affinity to populations from the lower Missouri River System in Missouri but not to populations from the Arkansas River System in southeastern Kansas. As *E. blennioides* is common in part of the Missouri River Basin to the east and southeast of the Kansas River its past occurrence upstream in the Flint Hills section of the Kansas River System cannot be ruled out. As some other species with Ozarkian affinities have entered the Kansas River System it is conceivable that *E. blennioides* also accomplished such an invasion only to be extirpated subsequent to settlement of the Basin.

SPECIES PROBABLY NOT OCCURRING IN THE KANSAS RIVER BASIN

These species have been reported in the literature, are not supported by specimens, and, as set forth below, are thought not to have occurred in the Kansas River Basin within historic time.

Several of these doubtful records were introduced into the literature by Cope (1864, 1865, 1871), who based his reports on specimens collected by

Dr. W. A. Hammond. Hammond was a surgeon assigned to an expedition under the command of Lt. F. T. Bryan. The itinerary of this expedition was summarized by Olund and Cross (1961:331). The expedition traversed parts of the drainages of the Kansas, Platte, and Green (of Wyoming) rivers in a journey from Fort Riley, Kansas to Bridgers Pass, Wyoming, and back. The assortment of fishes listed by Cope (1864, 1865, 1871) from "Kansas" or from "Platte River near Fort Riley" seem not to have come from a single locality or even from a single stream system. Some entries in the catalogue of the Division of Mammals, United States National Museum, suggest how the designation "Platte River near Fort Riley" might have originated—for example:

3040—Platte R.—236 miles from Fort Riley—June 27
3041—Platte R.—248 miles from Fort Riley—June 29
3042—Platte R.—350 miles from Fort Riley—July 4

Data entered in the catalogue and on labels of the Division of Fishes, United States National Museum, give the following localities from which collections were made (attributed to the expedition of Bryan) and illustrate the variations that have crept into the records concerning these old collections:

1. "Stranger's Creek, Kansas."
2. "Fort Riley"; "Fort Riley, Kansas."
3. "Republican R."; "Republican trib."; "Republican Fk."
4. "Pole Creek"; "Pole Creek, Neb."; "Pole Creek, Wyoming"; "Pole Cr.—Ft. Riley"; "Pole Creek, Cheyenne Pass."
5. "Bridger's Pass"; "Nr. Bridger's Pass"; "Wagon Road to Bridger's Pass."
6. "Kansas."

Entosphenus lamottenii (LeSueur). [As *Ammocoetes niger* Rafinesque by Cragin (1885b:106) and Graham (1885a:70).] Probably this record has resulted from misidentification. That Graham's specimen was not a brook lamprey is indicated by its being found attached to a "red-horse." Hubbs and Trautman (1937:73) placed these records in the synonymy of *Ichthyomyzon castaneus.*

Lepisosteus spatula Lacépède. [As *Litholepis tristoechus* (Bloch and Schneider) by Cragin (1885b:106).] Possibly this record refers to a large specimen of *Lepisosteus osseus.* The alligator gar, a southern species, probably approaches no nearer to the Kansas River Basin than the St. Louis area (Forbes and Richardson, 1906:35). Fisher (1962) did not find it in the lower Missouri River.

Salmo clarki Richardson. [As *Trutta lewisi* (Girard) by Cope (1865:85) and as *Salmo (Salar) stomias* Cope by Cope (1871).] These records were allocated to *Salmo mykiss stomias* by Everman and Cox (1896:356-357). I agree with Evermann and Cox (1896:355) that ". . . the trout mentioned as *Trutta lewisi* probably came from some point in the headwaters of the South Platte rather than from Fort Riley."

Umbra limi (Kirtland). To my knowledge, there is no evidence that the mudminnow has occurred, in historic time, in the Kansas River Basin despite inclusion of Kansas in the range of the species by some writers (Eddy and Surber, 1947:183; Moore, 1957:72). Probably it ranged farther south than at present during glacial stages of the Pleistocene.

Gila robusta Baird and Girard. [As *Gila affinis* Abbott by Abbott (1861:474) and Cope (1865:85).] Abbott's 1861:474) description of *G. affinis* (= *G. robusta)* list it from "Kansas." Evermann and Cox (1896:355) and Fowler (1925:397-398) pointed out that *Gila robusta* does not occur in the Missouri River Basin. It is, however, native to the upper Green River in Wyoming (Simon, 1946:79) in the area visited by the expedition of Lt. F. T. Bryan. An old label of red-bordered heavy paper, possibly the original label, with the type specimen (PAS 4196), states "*Gila affinis* (Abbott)—Dr. Ham-

mond—Bridger Pass." Another label, newer in appearance, bears the data "TYPE of *Gila affinis* Abbott ("Kansas") Bridger Pass, Green River basin, Wyoming. Dr. Wm. A. Hammond."

Rhinichthys cataractae (Valenciennes). [As *Rhinichthys maxillosus* Cope by Cope (1864:278 and 1865:85).] Cope's (1864:278) description of *R. maxillosus* (= *R. cataractae*) lists it from "Kansas." His later account (1865:85) includes it in a list of fishes from "Platte River, near Fort Riley." *Rhinichthys cataractae* occurs in the Platte Drainage but not in the Kansas River Drainage at the present time and there are no other records of the species from the Kansas River System. As the expedition under the command of F. T. Bryan traveled extensively in the Platte Drainage, it seems highly probable that "*Rhinichythys maxillosus*" was taken in that drainage.

Minytrema melanops (Rafinesque). [Reported by Cragin (1885b:108) from Mill Creek and Osage River.] To my knowledge there are no records of the spotted sucker from the Missouri River Basin other than those listed by Cragin. *Ptychostoma haydeni* Girard from the Upper Missouri River, although ascribed to *M. melanops* by some writers, has been shown to be *Moxostoma macrolepidotum* by Robins and Raney (1957:154).

Erimyzon sucetta (Lacépède). [Listed by Cragin (1885b:108) from "Kansas R. (Snow)."] According to distributional maps prepared by the Missouri Conservation Commission (courtesy of Mr. William Pflieger) neither this species nor *Erimyzon oblongus* (Mitchill) occurs in the Missouri River Basin in Missouri; nor is either species known elsewhere in the Basin.

Fundulus diaphanus (LeSueur). [Listed by Graham (1885a:75) from "Kansas River."] This record is far south and west of the present limits of the range of the banded killifish. Possibly Graham confused this killifish with *F. kansae*, a variable, sexually dimorphic species that does occur in the Kansas River.

Culaea inconstans (Kirtland). [As *Gasterosteus micropus* Cope (1865:81, 85) from "Platte River, near Fort Riley."] There are, to my knowledge, no original records of the brook stickleback from the Kansas River Basin except the description of *G. micropus* by Cope. As pointed out above, there is doubt whether Cope's specimens were collected in the Kansas or in the Platte river systems. As *C. inconstans* occurs in the Platte System it seems safer to suppose that Cope's material came from that system. Possibly the species existed farther south in the Plains during Pleistocene pluvial periods when its favored habitat of shallow ponds with aquatic vegetation might have been more widespread in this area of reatively low relief.

Roccus mississippiensis (Jordan and Evermann). [Listed by Cragin, (1885b:111) on authority of Snow but not reported by Snow (1875).] To my knowledge this is the sole record from the Kansas River Basin for the yellow bass. Probably it refers to *Roccus chrysops*, which seems to have been native to the Basin. *R. mississippiensis* has been widely introduced (Graham, 1885a: 78) and its occurrence in the Basin would not be surprising.

Ammocrypta pellucida (Baird). [Listed by Cragin (1885b:110) and Graham (1885b) from Kansas River and listed by Graham (1885a:76) from ". . . clear, sandy streams."] These records are far west of the range of *A. pellucida* (Moore, 1957:183; Linder, 1959:Fig. 1). Evermann and Cox (1896) listed no additional records of any species of *Ammocrypta* from the Missouri River Basin, nor did Fisher (1962) find any in the lower Missouri River. Two specimens (KSU 3415) of *Ammocrypta* in the collections of Kansas State University bear only the data "I. D. Graham." Although poorly preserved, these specimens seem assignable to *A. pellucida* (a few scales anteriorly on nape; opercle with broad, triangular spine; 6-8 scales below lateral line; five rows of scales from upper anterior corner of opercle to base of opercular spine; lateral-line scales 70 and 75; dorsal spines 10 and 11; anal spines and rays both I, 9).

Etheostoma cragini Gilbert. Regarding *E. cragini*, Gilbert (1887:63) wrote "A single specimen was also taken in Snokomo Creek, Wabaunsee County, Kansas." This is the sole record of this darter outside the Arkansas River Drainage. Gilbert's record seems in error, probably due to mixing of locality data or specimens from the Arkansas River System (reported in the same paper) with specimens from Snokomo Creek.

SUMMARY

Specimens of 71 species of fishes thought to be native were observed from the Kansas River System. The presence of seven species is known or believed to be entirely due to introduction by man. For six additional species evidence is inconclusive as regards native occurrence. There are records in the literature of eight species that may have inhabited the System in past, historic time but no longer occur there to the best of my knowledge.

Several areas, all possessing streams characterized by relatively clear and cool water and by rubbly, gravelly or sandy bottoms, were found to support a relatively diverse fish fauna. These areas were (1) the Shawnee Escarpments of northeastern Kansas, (2) the Flint Hills of northern Kansas, (3) an area in the western part of the Basin draining escarpments where the Ogallala Formation makes contact with underlying, aquicluding Cretaceous beds, and (4) an area in southern Nebraska along the north side of the Republican River Valley draining thick aquiferous deposits of Pleistocene sands and gravels. Species found principally in one or more of these areas were *Carpiodes velifer, Moxostoma erythrurum, Hybopsis biguttata, Chrosomus erythrogaster, Hybognathus hankinsoni, Notropis rubellus, Notropis cornutus, Notropis topeka, Pimephales notatus, Noturus exilis, Percina caprodes, Percina maculata, Etheostoma spectabile pulchellum, Ethostoma nigrum nigrum* and *Lepomis megalotis.*

At the opposite extreme were areas that supported few species of fish and in which streams were turbid, sometimes intermittent and possessed silty bottoms. Such areas included (1) an area mantled by glacial till in the northeastern part of the Basin; (2) an area (Loess Plains) mantled by thick deposits of loess in the northwestern part of the Basin in Nebraska (on the eastern margin of this area was a terrain, mantled both by glacial till and and by loess, that yielded the lowest number of species of any area in the Basin); (3) the "Dissected High Plains," an area in the central part of the Basin underlain by Cretaceous rocks of poor aquifying ability; and

(4) the Ogallala surface atop which all streams were observed to be highly intermittent, flowing only after rains. Ubiquitous species, especially characteristic of the areas, just mentioned, with the exception of (4), which has no permanent fauna in streams were *Notropis l. lutrensis, Notropis stramineus missuriensis, Pimephales promelas, Ictalurus melas* and *Lepomis cyanellus.*

Nineteenth-century accounts by visitors to the Kansas River Basin suggest that the larger streams fluctuated in amount of discharge and degree of turbidity then, as now. Tributaries, however, were probably clearer and more permanent than at present. The fauna both of the large and small streams seems to have changed to some extent. Early records from the lower mainstream indicate occurrence of species that, at present, rarely if ever ascend the Kansas River, although some of them still occur in the Missouri River. In this connection it should be noted that pollution has been intense in the lowermost mainstream. A number of species typical of tributaries (including several listed in Paragraph 2 of this Summary) seem to have been extirpated or their populations seem to have been decimated in much of the Basin, probably because of modifications of the watershed, especially agricultural modifications, that have resulted in increased intermittency, turbidity and siltation in these streams.

The occurrence of some species is best explained in terms of preglacial drainage patterns, of which three systems seem significant. One, the Preglacial Plains System, flowed southward, west of the Flint Hills of Kansas, extending at least as far north as the Platte or Niobrara rivers and draining southward into the Gulf of Mexico either by way of an ancestral equivalent of the Red River or by way of some other outlet on the coast of Texas. This system long drained the western part of the Kansas River System. That part of the Kansas River System east of the Flint Hills, on the other hand, drained eastward into another major preglacial drainage—that of the Teays/Mississippi System. A third preglacial system, far removed from the Kansas River Basin, but probably having some effect on the ichthyofauna of the Missouri River System, consisted of streams (extending southward as far as central South Dakota) draining northward into Hudson Bay.

From Pliocene fossil evidence and present distributions in the Great Plains it is hypothesized that species or subspecies that were contributed to the Kansas River System by the Preglacial Plains System (but not from other sources) were *Hybopsis gracilis*

gulonella, Notropis l. lutrensis, Notropis topeka, Notropis stramineus missuriensis, Hybognathus placitus, Phenacobius mirabilis, Fundulus kansae, Lepomis cyanellus, Lepomis humilis, and *Etheostoma spectabile pulchellum.*

In the course of glacial advances, some of the western drainage of Hudson Bay was deflected southward into the Great Plains and is thought to have made its way southward more or less along the course of the Preglacial Plains Stream (hereafter termed Ancestral Plains Stream). Species or subspecies that may have been in the preglacial Hudson Bay Drainage and that were deflected into the Ancestral Plains Stream include *Scaphirhynchus albus, Hybopsis meeki, Hybopsis gelida, Hybopsis gracilis gracilis, Hybognatus hankinsoni,* and *Moxostoma m. macrolepidotum.*

In epochs after retreat of the Kansan Glacier much downcutting westward by tributaries of the Mississippi River System caused several of those streams to reach the Ancestral Plains Stream, capture various segments of it, and thus fragment the System. The Kansas River had such an origin, with a tributary of the Missouri/Mississippi System cutting through the Flint Hills and capturing streams to the west. Outflow of the Kansas River to the Mississippi gave ready access to the Basin for a large number of fishes that inhabited the Ancetral Teays/Mississippi System.

Some species, especially those of larger rivers, probably reached the Kansas River Basin from two or three of the drainages noted above. Some species that have variational patterns, in the Great Plains and Interior Lowlands, suggestive of such a multiple origin are *Hybopsis aestivalis, Semotilus atromaculatus, Notropis atherinoides, Notropis blennius, Notropis stramineus, Pimephales promelas, Campostoma anomalum, Carpiodes cyprinus, Catostomus commersoni, Ictalurus melas,* and *Etheostoma spectabile.*

A mingling of eastern, western and northern stocks in the Great Plains and Interior Lowlands seems to have resulted from the disruptions and diversions of Pleistocene drainages, and from extirpation from, and reinvasion of, glaciated areas. Thus, differences that might once have distinguished populations of the Ancentral Plains System from eastern or northern populations were, in many cases, obscured. In only a few cases do northeastern and southwestern congeners seem to have attained the status of species (for example, *Hybognathus nuchalis* and *Hybognathus placitus*). In other cases well-defined subspecies exist in the northeast and in

the southwest (for example, *Etheostoma s. spectabile* and *E. s. pulchellum; N. s. stramineus* and *N. s. missuriensis*). In an even larger number of cases differences are of lesser degree from southwest to northeast and a wide zone of intergradation exists between the extremes.

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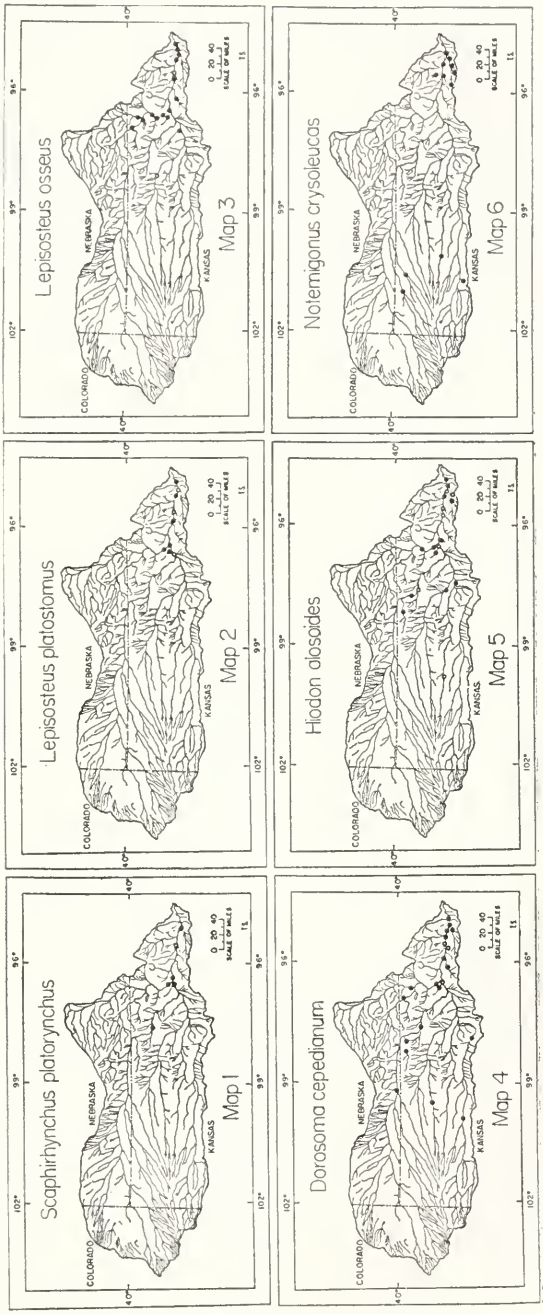
EXPLANATION OF MAPS

The localities of occurrence known for 51 species of fishes in the Kansas River Basin are shown in Maps 1-51. Circles indicate records prior to 1915; solid dots indicate records subsequent to 1915.



Hybopsis gracilis
Map 9
Chrosomus erythrogaster
Map 8
Semotilus atromaculatus
Map 7
Hybopsis meeki
Map 12
Hybopsis storeriana
Map 11
Hybopsis bigutlata
Map 10
Phenacobius mirabilis
Map 15
Hybopsis gelida
Map 14
Hybopsis aestivalis
Map 13
COLORADO
NEBRASKA
KANSAS
0 20 40
SCALE OF MILES

Notropis umbratilis
Map 18
Notropis rubellus
Map 17
Notropis atherinoides
Map 16
Notropis blennius
Map 21
Notropis lutrensis
Map 20
Notropis cornutus
Map 19
Notropis topeka
Map 24
Notropis stramineus
Map 23
Notropis buchanani
Map 22
COLORADO
NEBRASKA
KANSAS
0 20 40
SCALE OF MILES

Hybognathus hankinsoni
Map 25
Pimephales notatus
Map 26
Pimephales promelas
Map 27
Campostoma anomalum
Map 28
Ictiobus cyprinellus
Map 29
Ictiobus bubalus
Map 30
Carpiodes velifer
Map 31
Carpiodes carpio
Map 32
Moxostoma erythrurum
Map 33
COLORADO
NEBRASKA
KANSAS
102°
99°
96°
40°
0 20 40
SCALE OF MILES

Moxostoma macrolepidotum
Map 34
Catostomus commersoni
Map 35
Ictalurus punctatus
Map 36
Ictalurus natalis
Map 37
Ictalurus melas
Map 38
Noturus flavus
Map 39
Noturus exilis
Map 40
Pylodictis olivaris
Map 41
Anguilla rostrata
Map 42
COLORADO
NEBRASKA
KANSAS
0 20 40
SCALE OF MILES

Fundulus kansae
Map 43
Roccus chrysops
Map 44
Lepomis cyanellus
Map 45
Lepomis megalotis
Map 46
Lepomis humilis
Map 47
Percina caprodes
Map 48
Etheostoma nigrum
Map 49
Etheostoma spectabile
Map 50
Aplodinotus grunniens
Map 51
COLORADO
NEBRASKA
KANSAS
0 20 40
SCALE OF MILES

LITERATURE CITED

Abbott, C. C.
1861. Descriptions of four new species of North American Cyprinidae. Proc. Acad. Nat. Sci. Philadelphia, 1860:473-474.

1861. Descriptions of two new species of *Pimelodus,* from Kansas. Proc. Acad. Nat. Sci. Philadelphia, 1860:568-569.

Adams, F. G.
1904. Reminiscences of Frederick Chouteau. Trans. Kansas State Hist. Soc., 8:423-434.

Alden, W. C.
1924. Physiographic development of the northern Great Plains. Geol. Soc. America Bull., 35:385-424, September 30.

Al-Rawi, A. H. and Cross, F. B.
1964. Variation in the plains minnow, *Hybognathus placitus* Girard. Trans. Kansas Acad. Sci., 67(1):154-168, June 12.

Aughey, S.
1877. Catalogue of the land and fresh-water shells of Nebraska. Bull. U. S. Geol. and Geogr. Surv. Territories, 3(3):697-704, May 15.

Bailey, R. M.
1954. Distribution of the American cyprinid fish *Hybognathus hankinsoni* with comments on its original description. Copeia, 1954(4):289-291, October 29.

1956. A revised list of the fishes of Iowa, with keys for identification *in* Iowa Fish and Fishing. Iowa Conserv. Comm., Des Moines, pp. 327-377.

1959a. Distribution of the American cyprinid fish *Notropis anogenus.* Copeia, 1959(2):119-123, July 24.

1959b. Parasitic lampreys (*Ichthyomyzon*) from the Missouri River, Missouri and South Dakota. Copeia, 1959(2):162-163, July 24.

Bailey, R. M. and Allum, M. O.
1962. Fishes of South Dakota. Misc. Publ. Mus. Zool. Univ. Michigan, 119:1-131, June 5.

Bailey, R. M. and Cross, F. B.
1954. River sturgeons of the American genus *Scaphirhynchus:* characters, distribution, and synonymy. Papers Michigan Acad. Sci., Arts and Letters, 39:169-208, May 5.

Bailey, R. M. and Gosline, W. A.
1955. Variation and systematic significance of vertebral counts in the American fishes of the family Percidae. Misc. Publ. Mus. Zool. Univ. Michigan, 93:1-44, September 28.

Bailey, R. M., Winn, H. E. and Smith, C. L.
1954. Fishes from the Escambia River, Alabama and Florida, with ecologic and taxonomic notes. Proc. Acad. Nat. Sci. Philadelphia, 106:109-164, December 17.

Barlow, G. W.
1961. Causes and significance of morphological variation in fishes. Syst. Zool., 10(3):105-117.

Bayne, C. K.
1956. Geology and ground-water resources of Sheridan County, Kansas. Kansas Geol. Surv. Bull., 116:1-94, May 15.

Bayne, C. K. and Fent, O. S.
1963. The drainage history of the upper Kansas River Basin. Trans. Kansas Acad. Sci., 66(3):363-377, December 17.

Bayne, C. K., Walters, K. L. and Plummer, N.
1959. Geology and ground-water resources of Cloud County, Kansas. Kansas Geol. Surv. Bull., 139:1-144, May.

Berry, D. W. and Drumm, W. H.
1952. Geology and ground-water resources of Lincoln County, Kansas. Kansas Geol. Surv. Bull., 95:1-96, July.

Bradley, E. and Johnson, C. R.
1957. Geology and ground-water hydrology of the valleys of the Republican and Frenchman rivers, Nebraska. U. S. Geol. Surv. Water-supply Paper, 1360-H:iv + 589-713.

Bradley, E., Johnson, C. R. and Krieger, R. A.
1957. Ground-water resources of the Ladder Creek area in Kansas. Kansas Geol. Surv. Bull., 126:1-94, December.

Branson, B. A.
1963. Additions to and distributional annotations on the Kansas gastropod fauna. Trans. Kansas Acad. Sci., 66(1):72-75, May 9.

Branson, B. A. and Moore, G. A.
1962. The lateralis components of the acoustico-lateralis system in the sunfish family Centrarchidae. Copeia, 1962(1):1-108, April 11.

Breukelman, J.
1940a. The fishes of northwestern Kansas. Trans. Kansas Acad. Sci., 43: 367-376.
1940b. A collection of Kansas fishes in the State University Museum. Trans. Kansas Acad. Sci., 43:377-384.
1946. A review of Kansas ichthyology. Trans. Kansas Acad. Sci., 49(1): 51-70, August 6.

Caldwell, M. B.
1937. Exploring the Solomon River Valley in 1869. Kansas Hist. Quart., 6(1):60-76.

Call, R. E.
1885. Contributions to a knowledge of the fresh-water Mollusca of Kansas. II. Fresh-water univalves. Bull. Washburn College Lab. Nat. Hist., 1(2):51-54, February 15.
1886. Fifth contribution to a knowledge of the fresh-water Mollusca of Kansas. Bull. Washburn College Lab. Nat. Hist., 1(6):177-184, July.
1887. Sixth contribution to a knowledge of the fresh-water Mollusca of Kansas. Bull. Washburn College Lab. Nat. Hist., 2(8):11-25, November 2.

Carey, J. C.
1954. *Juniata:* Gateway to Mid-Kansas. Kansas Hist. Quart., 21(2): 87-94.

Chaney, R. W. and Elias, M. K.
1936. Late Tertiary floras from the High Plains. Carnegie Inst., Washington Publ., 476:1-72, October.

Cleary, R. E.
1956. The distribution of the fishes of Iowa *in* Iowa fish and fishing. Iowa Conserv. Comm., Des Moines, pp. 267-324.

Colby, C. C. and others
1956. The Kansas Basin, pilot study of a watershed. Univ. Kansas Press, Lawrence, x + 103 pp., September.

CONDRA, G. E. and REED, E. C.
1950. Correlation of the Pleistocene deposits of Nebraska (Rev.). Nebraska Geol. Surv. Bull., 15A:1-74, March.
1959. The geological section of Nebraska. Nebraska Geol. Surv. Bull., 14A:viii + 82.

COOK, F. A.
1959. Freshwater fishes in Mississippi. Hederman Bros., Jackson, Mississippi, 239 pp.

COPE, E. D.
1864. Partial catalogue of the cold-blooded Vertebrata of Michigan, Part I. Proc. Acad. Nat. Sci. Philadelphia, 1864:276-285.
1865. Partial catalogue of the cold-blooded Vertebrata of Michigan, Part II. Proc. Acad. Nat. Sci. Philadelphia, 1865:78-88.
1871. Recent reptiles and fishes *in* Report on the reptiles and fishes obtained by the naturalists of the expedition. Preliminary Rept. Geol. Surv. of Wyoming and portions of contiguous territories, being a second annual report of progress, 8:432-442.

CRAGIN, F. W.
1885a. Note on the chestnut lamprey. Bull. Washburn College Lab. Nat. Hist., 1(3):99-100, April 4.
1885b. Preliminary list of Kansas fishes. Bull. Washburn College Lab. Nat. Hist., 1(3):105-111, May 2.

CREVECOEUR, F. F.
1903. A new species of fish. Trans. Kansas Acad. Sci., 18:177-178.
1908. A new species of Campostoma? Trans. Kansas Acad. Sci., 21: 155-157.

CROSS, F. B.
1953. Occurrence of the sturgeon chub, *Hybopsis gelida* (Girard) in Kansas. Trans. Kansas Acad. Sci., 56(1):90-91.

CROSS, F. B. and HASTINGS, C. E.
1956. Ages and sizes of 29 flathead catfish from the Kansas River, Douglas County, Kansas. Trans. Kansas Acad. Sci., 59(1):85-86, April 12.

CROSS, F. B. and METCALF, A. L.
1963. Records of three lampreys (*Ichthyomyzon*) from the Missouri River System. Copeia, 1963(1):187, March 30.

DALQUEST, W. W.
1964. *Equus scotti* from a high terrace near Childress, Texas. Texas Jour. Sci., 16(3):350-358, September.
1965. New Pleistocene formation and local fauna from Hardeman County, Texas. Jour. Paleont., 39(1):63-79, January.

DAVIS, S. N.
1951. Studies of Pleistocene gravel lithologies in northeastern Kansas. Kansas Geol. Surv. Bull., 90(7):173-192, September 30.

DEACON, J. E.
1961. Fish populations, following a drought, in the Neosho and Marais des Cygnes rivers of Kansas. Univ. Kansas Publ. Mus. Nat. Hist., 13(9):359-427, August 11.

DEACON, J. E. and METCALF, A. L.
1961. Fishes of the Wakarusa River in Kansas. Univ. Kansas Publ. Mus. Nat. Hist., 13(6):309-322, February 10.

DEEVEY, E. S. JR.
1949. Biogeography of the Pleistocene. Part I: Europe and North America. Geol. Soc. America Bull., 60:1315-1416, September.

Distler, D. A. and Metcalf, A. L.
1962. *Etheostoma pallididorsum*, a new percid fish from the Caddo River System of Arkansas. Copeia, 1962(3):556-561, September 28.

Dyche, L. L.
1914. Ponds, pond fish, and pond fish culture. Kansas State Dept. Fish and Game Bull., 1:viii + 208 pp.

Eddy, S. and Surber, T.
1947. Northern fishes with special reference to the upper Mississippi Valley. (Second Ed.). University of Minnesota Press, Minneapolis, xii + 276 pp.

Ellis, M. M.
1914. Fishes of Colorado. Univ. Colorado Studies, 11(1):1-136, March.

Evermann, B. W. and Cox, U. O.
1896. Report upon the fishes of the Missouri River Basin. Rept. Comm. Fish and Fisheries, 20:325-429, November 27.

Fenneman, N. M.
1931. Physiography of western United States. McGraw-Hill Book Co., New York, xiv + 534 pp.

Fishel, V. C., Lohman, S. W. and Stoltenberg, H. A.
1948. Ground-water resources of Republic County and northern Cloud County, Kansas. Kansas Geol. Surv. Bull., 73:1-191, May.

Fisher, H. J.
1962. Some fishes of the lower Missouri River. Amer. Midl. Nat., 68(2): 424-429, October.

Fitch, H. S. and McGregor, R. L.
1956. The forest habitat of the University of Kansas Natural History Reservation. Univ. Kansas Mus. Nat. Hist. Misc. Publ., 10(3): 77-127, December 31.

Flint, R. F.
1955. Pleistocene geology of eastern South Dakota. U. S. Geol. Surv. Prof. Paper, 262:vi + 173.

1957. Glacial and Pleistocene geology. John Wiley and Sons, Inc., New York, xiv + 553 pp.

Forbes, S. A. and Richardson, R. E.
1909. The fishes of Illinois. Illinois Nat. Hist. Surv. Div., cxxxii + 357 pp.

Fowler, H. W.
1925. Notes on North American cyprinoid fishes. Proc. Acad. Nat. Sci. Philadelphia, 76:389-416, February 15.

Frye, J. C.
1955. The erosional history of the Flint Hills. Trans. Kansas Acad. Sci., 58(1):79-86, March 26.

Frye, J. C. and Fent, O. S.
1947. The late Pleistocene loesses of central Kansas. Kansas Geol. Surv. Bull., 70:29-52, September 15.

Frye, J. C. and Leonard, A. B.
1951. Stratigraphy of the late Pleistocene loesses of Kansas. Jour. Geol., 59(4):287-305, July.

1952. Pleistocene geology of Kansas. Kansas Geol. Surv. Bull., 99:1-230, November.

1957. Studies of Cenozoic geology along eastern margin of Texas High Plains, Armstrong to Howard counties. Bur. Econ. Geol., Univ. Texas Rept. Invest., 32:1-62, November.

1959. Correlation of the Ogallala Formation (Neogene) in western Texas with type localities in Nebraska. Bur. Econ. Geol., Univ. Texas Rept. Invest., 39:1-46, August.

1963. Pleistocene geology of Red River Basin in Texas. Bur. Econ. Geol., Univ. Texas Rept., Invest., 49:1-48, January.

FRYE, J. C., LEONARD, A. B. and SWINEFORD, A.
1956. Stratigraphy of the Ogallala Formation (Neogene) of northern Kansas. Kansas Geol. Surv. Bull., 118:1-92, March.

FRYE, J. C. and WILLMAN, H. B.
1960. Classification of the Wisconsinan Stage in the Lake Michigan Glacial Lobe. Illinois Geol. Surv. Circ., 285:1-16.

GERKING, S. D.
1945. The distribution of the fishes of Indiana. Invest. Indiana Lakes and Streams, 3:1-137.

GIBBS, R. H.
1957. Cyprinid fishes of the subgenus *Cyprinella* of *Notropis*. I. Systematic status of the subgenus *Cyprinella*, with a key to the species exclusive of the *lutrensis-ornatus* complex. Copeia, 1957(3):185-195, August 26.

GILBERT, C. H.
1884. Notes on the fishes of Kansas. Bull. Washburn College Lab. Nat. Hist., 1(1):10-16, September 8.

1885a. Description of three new fishes from Kansas. Proc. U. S. Nat. Mus., 7:512-514, January 19.

1885b. Second series of notes on the fishes of Kansas. Bull. Washburn College Lab. Nat. Hist., 1(3):97-99, April 4.

1886. Third series of notes on Kansas fishes. Bull. Washburn College Lab. Nat. Hist., 1(7):207-211, December.

1887. Descriptions of new and little known etheostomids. Proc. U. S. Nat. Mus., 10:47-64, May 17.

1889. Fourth series of notes on the fishes of Kansas. Bull. Washburn College Lab. Nat. Hist., 2(9):38-43, February.

GILBERT, C. R.
1961. Hybridization versus intergradation: an inquiry into the relationship of two cyprinid fishes. Copeia, 1961(2):181-192, June 19.

GILBERT, C. R. and BAILEY, R. M.
1962. Synonymy, characters, and distribution of the American cyprinid fish *Notropis shumardi*. Copeia, 1962(4):807-819, December 31.

GILE, W. S.
1885. Fish culture. Kansas State Board Agric. 4th Bienn. Rept., 1883-1884:643-644.

GILL, T.
1862. Descriptions of new species of Pimelodinae, Proc. Boston Soc. Nat. Hist., 8:42-46.

1864. Proceedings of June 7 (Untitled). Proc. Acad. Nat. Sci. Philadelphia, 1864:151.

1876. Report on ichthyology. *In* Report of explorations across the Great Basin of the territory of Utah for a direct wagon-route from Camp Floyd to Genoa, in Carson Valley, in 1859, by Captain J. H. Simpson. Appendix L. War Dept., Washington, pp. 385-431.

GIRARD, C.
1856. Researches upon the cyprinoid fishes inhabiting the fresh waters of the United States of America, west of the Mississippi Valley, from specimens in the museum of the Smithsonian Institution. Proc. Acad. Nat. Sci. Philadelphia, 8:165-213.

1858. Fishes. *In* Explorations and surveys for a railroad route from the Mississippi River to the Pacific Ocean. War Dept., Washington, 400 pp.

Goodrich, C.
1939. Pleuroceridae of the Mississippi River Basin exclusive of the Ohio River System. Occas. Papers Mus. Zool. Univ. Michigan, 406:1-4, June 23.

Graham, I. D.
1885a. Preliminary list of Kansas fishes. Trans. Kansas Acad. Sci., 9:69-78.
1885b. Some Kansas fishes now in the College Museum. The Industrialist, 10(30):4, March 14.

Greene, A. R.
1906. The Kansas River—its navigation. Trans. Kansas State Hist. Soc., 9:317-358.

Greene, C. W.
1935. The distribution of Wisconsin fishes. Wisconsin Conserv. Comm., Madison, Wisconsin, 235 pp., June.

Grinnell, J.
1924. Geography and evolution. Ecology, 5:225-229, July 29.

Hall, E. R.
1946. Mammals of Nevada. Univ. California Press, Berkeley, California, xi + 710 pp., July 1.

Hanna, G. D.
1909. The Mollusca of Douglas County, Kansas, Gasteropoda. Nautilus, 23:81-82; 94-96.

Hanson, W. D. and Campbell, R. S.
1963. The effects of pool size and beaver activity on distribution and abundance of warm-water fishes in a north Missouri stream. Amer. Midl. Nat., 69(1):136-149, January.

Harlan, J. R. and Speaker, E. B.
1956. Iowa fish and fishing. Iowa Conserv. Comm., Des Moines, Iowa, 377 pp.

Hart, S. H. and Hulbert, A. B.
1932. Zebulon Pike's Arkansaw Journal: in search of the southern Louisiana Purchase boundary line (interpreted by his newly recovered maps). Stewart Comm., Colorado College and Denver Public Library, xcvi + 200 pp., December.

Hastings, C. E. and Cross, F. B.
1962. Farm ponds in Douglas County, Kansas, and their use in fish production. Univ. Kansas Mus. Nat. Hist. Misc. Publ., 29:1-21, May 17.

Hay, O. P.
1887. A contribution to the knowledge of the fishes of Kansas. Proc. U. S. Nat. Mus., 10:242-253, July 2.

Henderson, F. R.
1960. Beaver in Kansas. Univ. Kansas Mus. Nat. Hist. Misc. Publ., 26:1-85, December 16.

Heuts, M. J.
1947. Experimental studies on adaptive evolution in *Gasterosteus aculeatus* L. Evolution, 1(1):89-102, July 12.

Hibbard, C. W.
1960. An interpretation of Pliocene and Pleistocene climates in North America. Michigan Acad. Arts, Sci. and Letters, Rept. for 1959-60:5-30.

Hibbard, C. W., Frye, J. C. and Leonard, A. B.
1944. Reconnaissance of Pleistocene deposits in north-central Kansas. Kansas Geol. Surv. Bull., 52:1-28, February 20.

Hodson, W. G.
1959. Geology and ground-water resources of Mitchell County, Kansas. Kansas Geol. Surv. Bull., 140:1-132, April.

Hodson, W. G. and Wahl, K. D.
1960. Geology and ground-water resources of Gove County, Kansas. Kansas Geol. Surv. Bull., 145:1-126, June.

Horberg, L. and Anderson, R. C.
1956. Bedrock topography and Pleistocene glacial lobes in central United States. Jour. Geol., 64(2):101-116, March.

Hubbs, C. L.
1930. Materials for a revision of the catostomid fishes of eastern North America. Univ. Michigan Mus. Zool. Misc. Publ., 20:1-47, April 30.

1940a. Fishes from the Big Bend Region of Texas. Trans. Texas Acad. Sci., 23:3-12.

1940b. Speciation of fishes. Amer. Nat., 74:198-211.

1942. An atherinid fish from the Pliocene of Oklahoma. Jour. Paleont., 16(3):399-400, May 6.

1943. Criteria for subspecies, species and genera, as determined by researches on fishes. Ann. New York Acad. Sci., 44(2):109-121, June 8.

1945. Corrected distributional records for Minnesota fishes. Copeia, 1945(1):13-22, March 31.

1951a. The American cyprinid fish *Notropis germanus* Hay interpreted as an intergeneric hybrid. Amer. Midl. Nat., 45(2):446-454, March.

1951b. Identification of cyprinid fish reported from Kansas as *Squalius elongatus*. Trans. Kansas Acad. Sci., 54(2):190-192, June 15.

Hubbs, C. L. and Black, J. D.
1940. Status of the catostomid fish, *Carpiodes carpio elongatus* Meek. Copeia, 1940(4):226-230, December 27.

Hubbs, C. L. and Bonham, K.
1951. New cyprinid fishes of the genus *Notropis* from Texas. Texas Jour. Sci., 3(1):91-110, March 30.

Hubbs, C. L. and Greene, C. W.
1935. Two new subspecies of fishes from Wisconsin. Trans. Wisconsin Acad. Sci., Arts and Letters, 29:89-101.

Hubbs, C. L. and Lagler, K. F.
1958. Fishes of the Great Lakes Region. (Second Ed.). Bull. Cranbrook Inst. Sci., 26:xiii + 213.

Hubbs, C. L. and Ortenburger, A. I.
1929a. Further notes on the fishes of Oklahoma with descriptions of new species of Cyprinidae. Publ. Univ. Oklahoma Biol. Surv., 1(2): 15-43, April.

1929b. Fishes collected in Oklahoma and Arkansas in 1927. Publ. Univ. Oklahoma Biol. Surv., 1(3):45-112, April.

Hubbs, C. L. and Trautman, M. B.
1937. A revision of the lamprey genus *Ichthyomyzon*. Misc. Publ. Mus. Zool. Univ. Michigan, 35:1-109, June 14.

Hubbs, C. L. and Walker, B. W.
1942. Habitat and breeding behavior of the American cyprinid fish *Notropis longirostris*. Copeia, 1942(2):101-104, July 10.

Hubbs, Clark
1957. Distributional patterns of Texas fresh-water fishes. Southwestern Nat., 2(2-3):89-104, December 27.

Hubbs, Clark and Herzog, W. F.
1955. The distribution of the suckermouth minnow, *Phenacobius mirabilis*, in Texas. Texas Jour. Sci., 7(1):69-71, March.

Jennings, D.
1942. Kansas fish in the Kansas State College Museum at Manhattan. Trans. Kansas Acad. Sci., 45(4):363-366.

Johnson, C. R.
1958. Geology and ground-water resources of Logan County, Kansas. Kansas Geol. Surv. Bull., 129:1-177, May.

Johnson, C. R. and Keech, C. F.
1959. Geology and ground-water resources of the Big Blue River Basin above Crete, Nebraska. U. S. Geol. Surv. Water-supply Paper, 1474:vi + 94.

Jordan, D. S.
1891. Report of explorations in Colorado and Utah during the summer of 1889, with an account of the fishes found in each of the river basins examined. Bull. U. S. Fish. Comm., 9:1-40.

Jordan, D. S. and Evermann, B. W.
1896. The fishes of North and Middle America. Bull. U. S. Nat. Mus., 47(1):1-1240.

Koster, W. J.
1957. Guide to the fishes of New Mexico. Univ. New Mexico Press, Albuquerque, New Mexico, viii + 116 pp.

Lachner, E. A.
1952. Studies of the biology of the cyprinid fishes of the chub genus *Nocomis* of northeastern United States. Amer. Midl. Nat., 48(2): 433-466, September.

Lagler, K. F. and Bailey, R. M.
1947. The genetic fixity of differential characters in subspecies of the percid fish, *Boleosoma nigrum*. Copeia, 1947(1):50-59, April 20.

Langsdorf, E.
1950. The first survey of the Kansas River. Kansas Hist. Quart., 18(2): 146-158, May.

Latta, B. F.
1949. Ground-water conditions in the Smoky Hill Valley in Saline, Dickinson, and Geary counties, Kansas. Kansas Geol. Surv. Bull., 84: 1-152, October.

Leonard, A. B.
1959. Handbook of gastropods in Kansas. Univ. Kansas Mus. Nat. Hist. Misc. Publ., 20:1-224, November 2.

Leonard, A. B. and Frye, J. C.
1956. Cambiamenti climatici nei Great Plains. Quaternaria, 3:27-37.

Lewis, L. D. and Dalquest, W. W.
1957. A fisheries survey of the Big Wichita River System and its impoundments. Texas Game and Fish Comm. IF Rept. Ser., 2:1-64, February.

Linder, A. D.
1959. The American percid fishes *Ammocrypta clara* Jordan and Meek and *Ammocrypta pellucida* (Baird). Southwestern Nat., 4(4): 176-184, December 15.

Lohman, S. W. and Frye, J. C.
1940. Geology and ground-water resources of the "Equus beds" area in south central Kansas. Econ. Geol., 35(7):839-866.

Lueninghoener, G. C.
1947. The post-Kansan geologic history of the lower Platte Valley area. Univ. Nebraska Stud., New Ser., 2:1-82, September.

Lugn, A. L.
1935. The Pleistocene geology of Nebraska. Nebraska Geol. Surv. Bull., 2nd Ser., 10:1-223.

McCarraher, D. B.
1961. Extension of the range of Northern Pike (*Esox lucius*). Trans. Amer. Fish. Soc., 90(2):227-228, April.

Mead, J. R.
1906. The Saline River country in 1859. Trans. Kansas State Hist. Soc., 9:8-19.

Meek, S. E.
1884. Description of a new species of *Hybopsis* (*Hybopsis montanus*). Proc. U. S. Nat. Mus., 7(33):526-527, January 19.
1894. Notes on the fishes of western Iowa and eastern Nebraska. Bull. U. S. Fish. Comm., 14:133-138, November 22.
1904. The fresh-water fishes of Mexico north of the Isthmus of Tehuantepec. Publ. Field Columbian Mus., Zool. Ser., 5:1xiii + 252, August.

Meneley, W. A., Christiansen, E. A. and Kupsch, W. O.
1957. Preglacial Missouri River in Saskatchewan. Jour. Geol., 65(4):441-447, July.

Merriam, D. F. and Frye, J. C.
1954. Additional studies of the Cenozoic of western Kansas. Kansas Geol. Surv. Bull., 109(4):49-64, May 15.

Metcalf, A. L.
1959. Fishes of Chautauqua, Cowley and Elk counties, Kansas. Univ. Kansas Publ. Mus. Nat. Hist., 11(6):345-400, May 6.

Metcalf, A. L. and Distler, D. A.
1961. New distributional records for two species of crayfish. Trans. Kansas Acad. Sci., 64(4):353-356, January 5.

Miller, R. R.
1948. The cyprinodont fishes of the Death Valley System of eastern California and southwestern Nevada. Misc. Publ. Mus. Zool. Univ. Michigan, 68:1-155, April 20.
1955. An annotated list of the American cyprinodontid fishes of the genus *Fundulus*, with the description of *Fundulus persimilis* from Yucatan. Occas. Papers Mus. Zool. Univ. Michigan, 568:1-25, August 1.
1961. Speciation rates in some fresh-water fishes of western North America *in* Vertebrate Speciation, W. F. Blair, Editor. Univ. Texas Press, Austin, pp. 537-560.

Minckley, W. L.
1956. A fish survey of the Pillsbury Crossing Area, Deep Creek, Riley County, Kansas. Trans. Kansas Acad. Sci., 59(3):351-357, October 31.
1959. Fishes of the Big Blue River Basin, Kansas. Univ. Kansas Publ. Mus. Nat. Hist., 11(7):401-442, May 8.

Minckley, W. L. and Craddock, J. E.
1962. A new species of *Phenacobius* (Cyprinidae) from the upper Tennessee River System. Copeia, 1962 (2):369-377, July 20.

Minckley, W. L. and Cross, F. B.
1959. Distribution, habitat and abundance of the Topeka Shiner *Notropis topeka* (Gilbert) in Kansas. Amer. Midl. Nat., 61(1):210-217.
1960. Taxonomic status of the Shorthead Redhorse, *Moxostoma aureolum* (LeSueur) from the Kansas River Basin, Kansas. Trans., Kansas Acad. Sci., 63(1):35-39, April 6.

Minckley, W. L. and Deacon, J. E.
1959. Biology of the flathead catfish in Kansas. Trans. Amer. Fish. Soc., 88(4):344-355, October.

Montgomery, Mrs. F. C.
1928. Fort Wallace and its relation to the frontier. Coll. Kansas State Hist. Soc., 17:189-283.

Moore, G. A.
1950. The cutaneous sense organs of barbeled minnows adapted to life in the muddy waters of the Great Plains Region. Trans. Amer. Microscop. Soc., 69(1):69-95.
1957. Fishes. (Part II *in* Vertebrates of the United States by W. F. Blair and others). McGraw-Hill Book Co., Inc., New York, pp. 33-210.

Moore, R. C.
1949. Divisions of the Pennsylvanian System in Kansas. Kansas Geol. Surv. Bull., 83:1-203, November.

Needham, P. R. and Gard, R.
1959. Rainbow trout in Mexico and California with notes on the cutthroat series. Univ. California Publ. Zool., 67(1):1-124, September 25.

O'Connor, H. G.
1960. Geology and ground-water resources of Douglas County, Kansas. Kansas Geol. Surv. Bull., 148:1-200, December.

Olund, L. J. and Cross, F. B.
1961. Geographic variation in the North American cyprinid fish, *Hybopsis gracilis*. Univ. Kansas Publ. Mus. Nat. Hist., 13(7):323-348, February 10.

Osborn, H. F.
1931. Cope: master naturalist. Princeton Univ. Press, Princeton, New Jersey, xvi + 740 pp., April.

Ortenburger, A. I. and Hubbs, C. L.
1926. A report on the fishes of Oklahoma, with descriptions of new genera. Proc. Oklahoma Acad. Sci., 6:123-141.

Parker, H. N.
1911. Quality of the water supplies of Kansas. U. S. Geol. Surv. Water-supply Paper, 273:1-375.

Plummer, N. and Romary, J. F.
1942. Stratigraphy of the pre-Greenhorn Cretaceous beds of Kansas. Kansas Geol. Surv. Bull., 41:313-348, November 30.

Quinn, J. H.
1957. Paired river terraces and Pleistocene glaciation. Jour. Geol., 65(2): 149-166, March.
1958. Plateau surfaces of the Ozarks. Proc. Arkansas Acad. Sci., 11: 36-43.

Riggs, C. D. and Bonn, E. W.
1959. An annotated list of the fishes of Lake Texoma, Oklahoma and Texas. Southwestern Nat., 4(4):157-168, December 15.

ROBINS, C. R. and RANEY, E. C.
1957. Distributional and nomenclatorial notes on the suckers of the genus *Moxostoma*. Copeia, 1957 (2):154-155, July 15.

ROSS, R. D.
1958. Races of the cyprinid fish *Campostoma anomalum pullum* (Agassiz) in eastern United States. Virginia Agric. Expt. Sta. Tech. Bull., 136:1-20, September.

SCHOEWE, W. H.
1949. The geography of Kansas. Part II, Physical geography. Trans. Kansas Acad. Sci., 52(3):261-333, October 18.
1951. The geography of Kansas. Part III, Hydrogeography. Trans. Kansas Acad. Sci., 54(3):263-329, October 2.
1952. Coal resources of the Cretaceous System (Dakota Formation) in central Kansas. Kansas Geol. Surv. Bull., 96:69-156, February 29.

SIMON, J. R.
1946. Wyoming fishes. Wyoming Game and Fish Dept. Bull., 4:1-129.

SIMPSON, J. H.
1876. Report of explorations across the Great Basin of the territory of Utah for a direct wagon-route from Camp Floyd to Genoa, in Carson Valley, in 1859, by Captain J. H. Simpson. War Dept., Washington, 518 pp.

SLAUGHTER, B. H., CROOK, W. W., JR., HARRIS, R. K., ALLEN, D. C. and SEIFERT, M.
1962. The Hill-Shuler local faunas of the upper Trinity River, Dallas and Denton counties, Texas. Bur. Econ. Geol. Univ. Texas Rept. Invest., 48:viii + 75, December.

SMITH, C. L.
1954. Pleistocene fishes of the Berends Fauna of Beaver County, Oklahoma. Copeia, 1954(4):282-289, October 29.
1958. Additional Pleistocene fishes from Kansas and Oklahoma. Copeia, 1958(3):176-180, August 28.
1962. Some Pliocene fishes from Kansas, Oklahoma, and Nebraska. Copeia, 1962(3):505-520, September 28.

SMITH, G. R.
1963. A late Illinoian fish fauna from southwestern Kansas and its climatic significance. Copeia, 1963(2):278-285, June 14.

SMUCKER, S. M.
1856. The life of Col. John Charles Fremont, and his narrative of explorations and adventures, in Kansas, Nebraska, Oregon and California. Miller, Orton and Mulligan, New York and Auburn, 493 pp.

SNOW, F. H.
1875. The fishes of the Kansas River, as observed at Lawrence. Kansas State Board Agric., Annual Rept., 4:139-141.

STRAWN, K.
1961. A comparison of meristic means and variances of wild and laboratory-raised samples of the fishes *Etheostoma grahami* and *E. lepidum* (Percidae). Texas Jour. Sci., 13(2):127-159, June.

SWINEFORD, A. and FRYE, J. C.
1951. Petrography of the Peoria Loess in Kansas. Jour. Geol., 59(4): 306-322, July.

Swineford, A., Leonard, A. B. and Frye, J. C.
1958. Petrology of the Pliocene pisolitic limestone in the Great Plains. Kansas Geol. Surv. Bull., 130 (2):97-116, May 15.

Taylor, W. R.
1954. Records of fishes in the John N. Lowe collection from the Upper Peninsula of Michigan. Misc. Publ. Zool. Univ. Michigan, 87:1-50, November 9.

Thienemann, A.
1950. Verbreitungsgeschichte der Suesswassertierwelt Europas. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, xvi + 809 pp.

Thwaites, R. G.
1905a. Original journals of the Lewis and Clark expedition 1804-1806. Dodd, Mead and Co., New York, Vol. 5, ix + 395 pp., March.

1905b. Original journals of the Lewis and Clark expedition 1804-1806. Dodd, Mead and Co., New York, Vol. 6, ix + 280 pp., July.

1905c. Account of an expedition from Pittsburgh to the Rocky Mountains performed in the years 1819, 1820. By order of the Hon. J. C. Calhoun, Secretary of War, under the command of Maj. S. H. Long, of the U. S. Top. Engineers. The Arthur H. Clark Co., Cleveland, Ohio, Vol. 14, 321 pp.

1905d. Travels in the interior of North America by Maximilian, Prince of Wied. The Arthur H. Clark Co., Cleveland, Vol. 22, 393 pp.

1906a. Travels in the far West 1836-1841. II. Letters and sketches, with a narrative of a year's residence among the Indian tribes of the Rocky Mountains. By Father Pierre Jean de Smet S. J. The Arthur H. Clark Co., Cleveland, Vol. 27, pp. 123-411.

1906b. Journal of travels over the Rocky Mountains to the mouth of the Columbia River, made during the years 1845 and 1846. By Joel Palmer. The Arthur H. Clark Co., Cleveland, Vol. 30, 311 pp.

Todd, J. E.
1914. The Pleistocene history of the Missouri River. Science, n. s., 39:263-274, February 20.

1923. Is the channel of the Missouri River through North Dakota of Tertiary origin? Geol. Soc. America Bull., 34:469-494, September 30.

Trautman, M. B.
1956. *Carpiodes cyprinus hinei*, a new subspecies of carpsucker from the Ohio and upper Mississippi river systems. Ohio Jour. Sci., 56:33-40, January 18.

1957. The fishes of Ohio. Ohio State University Press, Columbus, Ohio, xviii + 683 pp.

Trautman, M. B. and Martin, R. G.
1951. *Moxostoma aureolum pisolabrum*, a new subspecies of sucker from the Ozarkian streams of the Mississippi River System. Occas. Papers Mus. Zool. Univ. Michigan, 534:1-10, November 12.

Underhill, J. C.
1957. The distribution of Minnesota minnows and darters in relation to Pleistocene glaciation. Minnesota Mus. Nat. Hist. Occas. Pap., 7:vi + 45.

Underhill, J. C. and Merrell, D. J.
1959. Intra-specific variation in the Bigmouth Shiner (*Notropis dorsalis*). Amer. Midl. Nat., 61(1):133-147, January.

Walters, K. L.
1956. Geology and ground-water resources of Rawlins County, Kansas. Kansas Geol. Surv. Bull., 117:1-100, June.

WEDEL, W. R.
1936. An introduction to Pawnee archeology. Bur. Amer. Ethnology Bull., 112:1-122.
1941. Environment and native subsistence economies in the central Great Plains. Smithson. Misc. Coll., 101(3):1-29, August 20.
1946. The Kansa Indians. Trans. Kansas Acad. Sci., 49(1):1-35, August 6.
1961. Prehistoric man on the Great Plains. Univ. Oklahoma Press, Norman, Oklahoma, xviii + 355 pp.

WILLIAMS, A. B.
1954. An explanation for the distribution of a North American crayfish. Ecology, 35(4):573-575.

YERGER, R. W. and SUTTKUS, R. D.
1962. Records of freshwater fishes in Florida. Tulane Stud. Zool., 9(5):323-330, April 16.

ZAHURANEC, B. J.
1962. Range extensions of some cyprinid fishes in southeastern Ohio. Copeia, 1962(4):842-843, December 31.

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Factors Affecting Growth and Production of Channel Catfish, Ictalurus punctatus

BY

BILL A. SIMCO AND FRANK B. CROSS

University of Kansas
Lawrence
1966

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Factors Affecting Growth and Production of Channel Catfish, Ictalurus punctatus

BY

BILL A. SIMCO AND FRANK B. CROSS

University of Kansas
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1966

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INTRODUCTION

The production of channel catfish, *Ictalurus punctatus* (Rafinesque), in small ponds has been under study by the State Biological Survey of Kansas since 1954. With the steadily increasing number of farm ponds in Kansas, there has been a growing interest in raising channel catfish for sport, food and profit. Six advantages of channel catfish as a pond-fish are:

1. Channel catfish are native, well-known to Kansas anglers, and are highly popular both as a sport- and table-fish.

2. They are tolerant of varied environmental conditions, including turbid water. Buck (1956:33) has shown that turbid water is not conducive to good growth and reproduction of bluegill and bass but that catfish do well in both clear and muddy water. Hastings and Cross (1962:20) reported that most ponds in Douglas County, Kansas, are too small and muddy to provide satisfactory angling for bass and bluegill, and suggested substitution of channel catfish in such ponds.

3. Channel catfish attain a large size; the record for the species exceeds 60 pounds. Occasionally, channel catfish weighing 25 pounds or more are caught from lakes in Kansas, and farm ponds have been known to produce channel catfish as heavy as 17 pounds. Although such large fish are unusual, they indicate the great capacity for growth that is an important attribute of any sport-fish. At normal rates of stocking, channel catfish attain a desirable size early in life; therefore, they are available for capture by anglers during a large part of their life-span.

4. Channel catfish are omnivorous and opportunistic in their feeding habits (Davis, 1959:6). Consequently they readily use supplemental feeds introduced in the ponds, making it possible to increase pond-production greatly.

5. Natural reproduction of channel catfish in ponds is not usually excessive (Marzolf, 1957:28; Davis, 1959:20-21; and others). Thus, knowledge of the approximate number of catfish in a pond is possible, and there is little likelihood of stunted growth due to overpopulation. Supplemental feed is utilized efficiently in rearing the fish to usable size. Techniques of propagation of catfish are well-developed (Morris, 1939; Brown, 1942; Canfield, 1947; Lenz, 1947; Clemens and Sneed, 1957; and Marzolf, 1957). Marzolf (1957) discusses methods by which natural reproduction in ponds can be assured if desired.

6. Fingerling channel catfish for stocking-purposes are available from State (Kansas Forestry, Fish and Game Commission, Pratt, Kansas), Federal (U. S. Fish and Wildlife Service, Farlington, Kansas), and several private hatcheries.

We investigated growth of channel catfish on "natural" food and on supplemental feeds, the effects of feeds differing in protein-level and source of carbohydrate, and the effects of stocking-rates and feeding-rates on production. Also, the physical-chemical situations existing in ponds will be considered and correlated with the growth of the catfish.

METHODS

The experiments to be discussed were made in ponds of the State Biological Survey of Kansas in Lawrence. These earth-fill, hatchery-style ponds are adjacent to one another and are alike in size and shape (1/10 acre, approximately 114 x 40 feet). Nine ponds (eight constructed in 1954 and one built in 1962) slope from a depth of two feet at one end to five feet at a drain-box in one corner of the opposite end. Two other ponds constructed in 1962 are subdivided transversely by means of hardware cloth (½ inch mesh, 6 feet high) recessed at least 12 inches in the pond-bottoms and dikes to prevent passage of fish; each of these two ponds contains four sections, 20 x 40 feet, has open areas at each end of the pond (Figure 1) and a bottom that slopes only one foot from the shallow end to the drain. The 11 ponds are filled and drained independently; the source of water is a reservoir of 20 acre-feet that receives runoff from grassland.

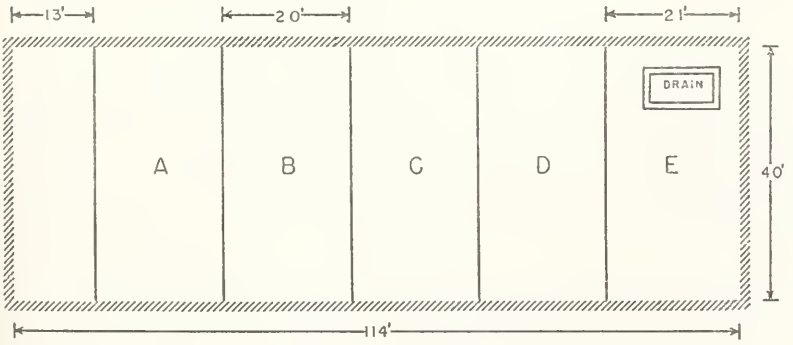

FIG. 1. Diagram of One of the Experimental Ponds (Ponds 10 and 11) that Were Subdivided by Hardware Cloth (Partitions Indicated by Vertical Lines). Area of Each Pond is 1/10 acre.

The ponds remained dry overwinter, except for ponds used to "hold" fish in that season. Ponds were filled and stocked with a known number of fish in spring, and the rate of growth was estimated by means of samples of fish seined at two-week intervals in summer. Replicated samples indicated that our sampling procedure was relatively consistent; t-tests detected no significant differences, at the 95 per cent level of probability, between samples taken from the same pond on the same day.

In autumn the ponds were drained and all surviving fish were recovered; their number and total weight were recorded, and individual lengths and weights were taken of 25 or more fish from each pond. Waterlevels and other factors subject to our control were the same in all ponds, except for variables (such as kind and rate of feeding) being tested.

In experiments on feeding of catfish, food was introduced at the same places in the ponds once daily at sundown. Channel catfish feed most actively from sundown to midnight (Bailey and Harrison, 1948:135-136). In experiments involving fertilization, liquid ammonium phosphate (8-25-0 formulation) was used at a rate of 50 pounds per acre per application.

Aquatic vegetation rarely grew excessively and was removed manually. Liquid fertilizer broadcast on the surface of ponds usually resulted in the formation of dense plankton-blooms within four days after application. High turbidity caused by the blooms usually restricted development of rooted and filamentous vegetation. The large poundages of fish present, and frequent seining of the ponds, also deterred the development of excessive vegetation.

Terminology and Abbreviations

Most of the terminology used in this report is the same as that in other works on fishery management; the more important terms, as they relate to our studies, can be defined as follows:

"Carrying capacity" is the maximum poundage of fish (one or more species) that a pond will support during a stated interval of time.

"Standing crop" is the poundage of fish (one or more species) that is present in a pond at a given time.

"Production" (gain) is the increase in the weight of fish during a designated period (normally one growing season).

"Yield" is the total poundage of fish obtained when a pond is drained. The above terms are expressed as pounds of fish per surface-acre of water (lbs./A).

"Fingerling" refers to a fish of the previous year's spawn; "subadult" refers to a two-year-old fish (one year older than fingerling).

In statistical analyses, the symbols "n.s.," "*," and "**" signify, respectively, non-significance, significance at the 95 per cent level of probability, and significance at the 99 per cent level of probability.

MORTALITY AND REPRODUCTION OF CHANNEL CATFISH IN PONDS

Mortalities in 41 experiments varied from 0 to 22 per cent (average of 5 per cent); mortalities in 1961-64 varied from 0 to 7 per cent.

Although spawning by channel catfish in small impoundments has been reported (Marzolf, 1957:22; Tiemeier, 1957:295; Davis, 1959:9), and has occurred in several private ponds under study by the State Biological Survey in eastern Kansas, no spawns of channel catfish have occurred in our experimental ponds. No suitable nest-sites are available in the experimental ponds, and most of the catfish used were less than three years old, the youngest age at which channel catfish normally spawn (Brown, 1942:311).

PRODUCTION OF CHANNEL CATFISH ON "NATURAL" FOODS

To ascertain production of channel catfish that subsisted solely on foods naturally available in our ponds, nine experiments were conducted without the addition of supplemental feed or fertilizer (Table 1).

Stocking-rates varied from 500 to 2250 fingerling catfish per acre. Except as noted (two cases, Table 1), channel catfish were the only fish in these ponds. In one growing season standing crops of 98 to 162 pounds of catfish per acre were obtained. The average standing crop was 131 pounds per acre. In four experiments conducted for two growing seasons, stocking-rates of 500, 510, 1000, and 1000 catfish per acre yielded 183, 182, 170 and 135 pounds per acre, respectively (average 168 pounds).

Several workers (Ball, 1952; Brown, 1951; Hansen *et al.*, 1960; Swingle, 1947) have reported increases in the standing crops of fishes, following the addition of various inorganic and organic fertilizers to ponds. Some kinds of fish receive greater benefits, or more direct benefits, from fertilization than do other species. We attempted to determine the effect of fertilization on the production of channel catfish (Table 1). Two ponds were stocked at rates of

TABLE 1.—PRODUCTION OF CHANNEL CATFISH IN PONDS (EACH 1/10 ACRE), WITHOUT EXTENSIVE SUPPLEMENTAL FEEDING.

Year	Pond number	Rate of stocking (per acre)	Mortality (per cent)	Fertilizer (pounds per acre)	Average weight (pounds)	Yield (pounds per acre)	Production (gain) (pounds per acre)
			At end of one growing season				
1963.....	9	2250	7	.....	0.05	108.7	78.5
1955.....	2	500	(18)	.....	.24	98.0	91.5
1963.....	6	750	3	.....	.15	115.3	92.2
1959.....	6	1000	(22)	.....	.14	109.0[1]	96.0
1958.....	5	700	4	.....	.16	107.5	98.4
1959.....	7	1000	(20)	.....	.14	112.0[2]	99.0
1963.....	1	2250	2	.....	.07	162.5	132.3
1958.....	3	700	1	†	.21	147.0	137.9
1958.....	2	700	1	†	.23	155.0	145.9
1959.....	5	750	4	200	.23	162.5	152.8
1959.....	4	700	1	500	.24	162.5	153.4
			At end of two or more growing seasons				
1959–60....	7	1000	20	.....	.17	135.0[2]	122.0
1959–60....	6	1000	22	.....	.22	170.3[1]	157.3
1955–56....	1	510	12	.....	.40	182.0	175.4
1955–57....	2	500	18	.....	.47	183.0	176.5

† Small quantities of feed placed on trays in the ponds were not eaten but may have had a fertilizing effect.

1. Contained bass, as well as channel catfish, in both first and second growing seasons, and bluegill in second growing season.

2. Contained bass and bluegill, in addition to channel catfish, in both first and second growing seasons.

700 to 750 fingerling catfish/A and were fertilized periodically in summer. On draining after one growing season, each pond yielded 162.5 pounds of catfish per acre. In two other ponds stocked at a rate of 700 catfish per acre, small amounts of feed (totaling approximately 30 pounds, or 300 pounds per acre, for the entire year) were placed on trays in the ponds. Observations of the trays indicated that this feed was not eaten, but it may have had a fertilizing effect in the ponds. These ponds yielded 147 and 155 pounds of catfish per acre when drained after one growing season.

In 1963 natural production of fish in relatively infertile ponds differed from that in fertile ponds. Pond No. 1 (built in 1954) had been fertilized in some years, and in feeding-experiments had yielded the highest productions obtained in any of our ponds;

therefore, it is considered a fertile pond. Pond No. 9 (constructed in 1962) was filled with water for the first time on the date of stocking, April 2, 1963. No fertilizer nor feed was added to either pond in 1963. The yields of catfish in these two ponds, when drained on October 16-17, 1963, were 162 pounds per acre in Pond No. 1, and 109 pounds per acre in Pond No. 9 (Table 20, p. 247). In Pond 1 catfish did not grow after August 12, when 193 pounds per acre were estimated to be present. The 162 pounds of fish per acre obtained in Pond 1 equals the poundage obtained earlier in ponds that were fertilized several times in the growing season of the fish being raised in those ponds. Seemingly, the production of catfish varied with the basic fertility of the ponds, and the time of application of fertilizer was unimportant in that the effects of fertilization carried over from previous years. The duration of such effects probably is limited; Tanner (1960) reports that ponds undergo reduction in their standing crop three or more years after fertilization is stopped.

The different stocking rates that were used did not affect the yields significantly. The highest poundages obtained on "natural" foods were in ponds stocked with 700 and 2250 catfish per acre. (Table 1). High stocking rates yielded large numbers of small fish having approximately the same total weight as fish stocked at lower rates.

The greatest poundage of catfish that our ponds will support without supplemental feeding (their carrying capacity) is less than 200 pounds per acre.

NUTRITIONAL ASPECTS OF FEEDING CHANNEL CATFISH

The nutritional requirements of fish only recently have been considered in detail, and such studies have dealt primarily with salmonids (Phillips *et al.*, 1963 and previous reports of the Cortland Hatchery; Halver and Coates, 1957). A few publications exist on the nutritional requirements of channel catfish (Nail, 1965; Shell, 1963).

Effects of synthetic diets on the growth of channel catfish were investigated in a concrete feeding-trough, 36 feet long. The trough is divided by screens into 24 compartments, each of which is 15 inches wide, 5 feet long and approximately 30 inches deep. Filtered tapwater flows continuously through the trough, entering at several points along the bottom and overflowing through several outlets near the top of the trough.

In preliminary investigations conducted in 1960, channel catfish were fed rations containing 10, 20, 30 and 40 per cent protein. The rations consisted of vitamin-free casein and dextrin in amounts that gave the desired protein-levels, plus a vitamin-mixture and Salts IV. The vitamin-mixture used was that recommended by Halver and Coates (1957) for rainbow trout; subsequently, we learned that the vitamin-requirements of channel catfish have been investigated by Dupree (unpublished doctoral dissertation, Auburn University, 1960). The amounts of casein and dextrin were adjusted to give the various protein-levels, with vitamins and salts constant in all rations.

Two methods of force-feeding were used—capsules and syringes. Gelatin capsules (size 00) filled with 1.5 grams of ration were forced into the stomach of the fish by means of forceps. Syringes used were of the 10 cc veterinary type having graduated plungers. These were modified by drilling out the needle-adapter so that alloy tubing of relatively large bore could be fitted to the syringe. The short section of metal tubing was tipped with flexible plastic tubing to minimize injury to the fish. The dry rations were diluted with distilled water to a semi-solid consistency that could be extruded through the tube, into the stomach of the fish.

Three channel catfish having an average weight of 94 grams were placed in each of 18 compartments, and fed once daily from August 13 to October 11, 1960. Each of the four rations was fed to fish in four compartments, two groups of fish by syringes and two by means of capsules. Two other groups of fish received a commercial food (Clark's Pond-fish Food, containing approximately

Table 2.—Average Gains (in Grams) of Channel Catfish Confined in Troughs, on Synthetic Diets Used in 1960.

Per Cent Protein in Ration	Feeding method	
	Syringe	Capsule
10	−11.3	17.9
20	−2.8	19.0
30	7.1	14.2
40	7.1	26.6
35 (Clark's)	−11.9	21.3

35 per cent protein), which was administered by both feeding-methods.

Growth by all fish was too slight (Table 2) to evaluate the effects of different protein-levels, possibly due to the short duration of the experiment (55 days) late in the growing season. Fish that were fed capsules consistently gained more weight than fish receiving the same food by means of syringe. The reasons for superiority of capsules may have been 1) undetected regurgitation of food administered by syringe, or 2) injury to the stomach-lining and interference with digestive processes of fish fed by syringe. When all fish were sacrificed after completion of the experiment, injury to the wall of the stomach was noted in only one fish fed by syringe. Our results indicate that in projects requiring force-feeding, capsules are preferable to syringes.

In 1961, synthetic diets containing 20, 40 and 60 percent protein were used. Fish that received the 10 per cent protein-ration in

TABLE 3.—COMPOSITION OF SYNTHETIC DIETS USED IN EXPERIMENTAL TROUGH, 1961 (QUANTITIES EXPRESSED AS PER CENT).

CONSTITUENT	Protein-level		
	20	40	60
Starch, sucrose, dextrin or cellulose	70.44	50.6	30.75
Casein	20.00	39.6	59.52
Salts IV	3.97	3.97	3.97
Corn Oil	4.96	4.96	4.96
Choline	0.79	0.79	0.79
Vitamins†			

† Vitamins as recommended by Dupree, unpublished doctoral dissertation, Auburn University, 1960.

	Amount		
Thiamin	6	Mg/100gm of casein	
Riboflavin	20	" "	
B^6	4	" "	
Niacin	80	" "	Mixed with casein
Calcium pantothenate	28	" "	
Inositol	200	" "	
Biotin	0.6	" "	
A	1	Gm/450gm oil	Mixed with oil
E	8	" "	

1960 had friable, discolored livers indicative of fatty metamorphosis; hence, we discontinued testing at this level and increased the upper limit of protein to 60 per cent. In addition, the carbohydrate constituent of the feed varied in 1961; cellulose, sucrose, dextrin, and starch were used (Table 3). The vitamin-mixture was that of Dupree (*loc. cit.*) rather than Halver and Coates (1957).

Because of poor growth by fish that were force-fed in the previous year, "ad-lib" feeding was attempted. The rations were diluted with distilled water, pressed through a pastry decorator (or caulking gun) into long strips and then allowed to dry on screens. When dry, the strips were broken into small pieces by hand. The rations were then weighed and placed loosely in each section of the trough.

Five fish (average weight = 17.7 grams, average length = 132 mm) were placed in each of 24 sections of the experimental trough. Each of the 12 rations was fed to fish in two compartments (a total of 10 fish) twice daily at the rate of approximately 5 per cent of body weight per day, from July 1 until October 16, 1961.

Gains made on the various diets are shown in Table 4. An analysis of variance demonstrated a significant difference (at the 95 per cent level of probability) in growth associated with the different protein-levels as well as with the type of carbohydrate present.

Source of variation	Degrees of freedom	Mean square	F
Among Protein-levels	2	2444.69	7.216 **
Among Carbohydrates	3	1830.52	5.403 *
Interaction	6	478.24	1.411 n.s.
Error	12	338.79	
Total	23		

Growth by our catfish correlated directly with the protein-level in most diets (Table 4). Differences in growth were mainly between the 20 and 40 per cent protein-rations (202 grams), while only 66 more grams were gained on the 60 per cent ration than on the 40 per cent ration. In studies by Nail (1965), the highest gains were made on a diet containing 34.8 per cent protein (the highest protein-level that Nail used), but growth of his fish on this feed was not significantly higher ($P \neq .95$) than that made on a diet containing 25.3 per cent protein.

Catfish that received feeds containing cellulose best reflected the positive effect of increased protein-content in the synthetic rations that we used (Table 4, Figure 2). We assume that channel catfish derive little energy from cellulose; thus, growth made on the diets containing cellulose was due to constituents other than carbohydrates. The other carbohydrates used in our rations (starch, dextrin, sucrose) modified the effect of increased protein-content,

TABLE 4.—WEIGHT-GAINS (GRAMS) BY CHANNEL CATFISH, CONFINED IN EXPERIMENTAL TROUGH, ON SYNTHETIC DIETS USED IN 1961.

PROTEIN-LEVEL	Source of carbohydrate					
	Cellulose	Sucrose	Dextrin	Starch	Total	Average
20	24.3	67.0	57.7	89.7		
	34.9	46.9	77.0	122.1		
	59.2	113.9	134.7	211.8	519.6	65.0
40	78.0	106.8	113.3	124.4		
	60.7	65.1	101.5	71.8		
	138.7	171.9	214.8	196.2	721.6	90.2
60	91.0	86.4	102.7	113.6		
	96.0	107.8	75.1	115.4		
	187.0	194.2	177.8	229.0	788.0	98.5
Total	384.9	480.0	527.3	637.0	2029.2	
Average	64.1	80.0	87.9	106.2		84.6

presumably due to their protein-sparing action. Nail (*loc. cit.*) calculated that 0.23 grams of carbohydrate spared 0.05 grams of protein per hundred grams of fish from use for energy by his channel catfish. The kind of carbohydrate had little effect on the growth made by channel catfish on our diets containing 60 per cent protein, presumably because that amount of protein was so high that additional energy in the form of carbohydrates was not needed. In rations containing lower levels of protein, the amount and kind of carbohydrate were important.

Starch, dextrin, and sucrose were utilized by channel catfish, but were not equally beneficial. More growth was made by our fish on diets containing starch than on diets containing dextrin, and growth on the dextrin-rations exceeded growth on diets containing sucrose (Table 4, Figure 2). This relationship is opposite to that reported for chinook salmon by Buhler and Halver (1961:316), who found that "fish growth decreased considerably with increasing carbohydrate molecular weight."

In explanation of the differences in growth that were associated with the kind of carbohydrate in our tests two possibilities occur to us.

First, more rapid dissolution of sucrose than of the less soluble dextrin and starch, before ingestion of the rations by the fish, may

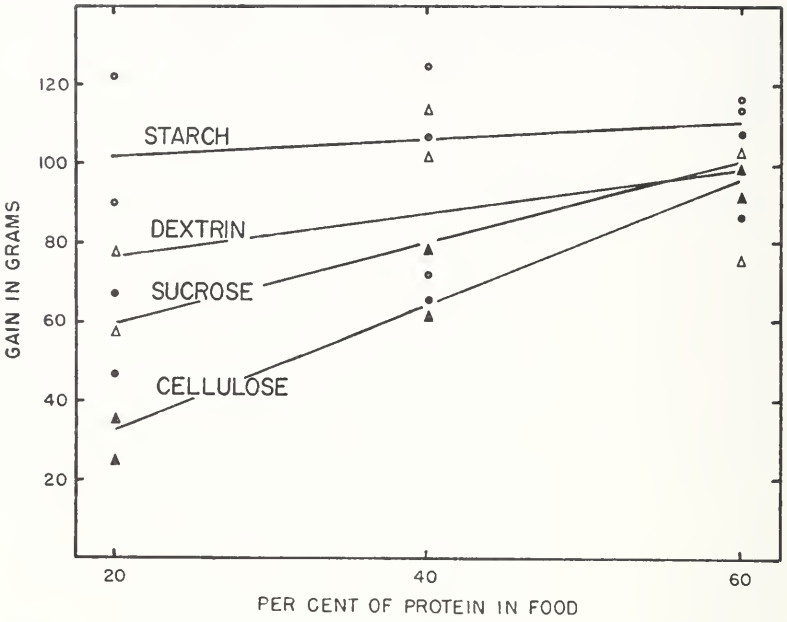

FIG. 2. Gains (in Grams) Made by Fingerling Channel Catfish on Synthetic Rations Containing Different Forms of Carbohydrate, while Confined in Experimental Trough from July 1 to October 16, 1961. Lines are Regressions on Absolute Gains Made by Duplicate Groups of Catfish on Each Protein-level (20, 40, and 60 Per Cent). Open Circles Represent Rations Containing Starch; Open Triangles, Dextrin; Solid Circles, Sucrose; Solid Triangles, Cellulose.

have reduced the food-value actually received by fish on the sucrose diet. Tunison *et al.* (1939:11) noted that loss of sucrose by dissolution affected their results in feeding tests using brook trout.

Second, the amount of digestible carbohydrate used in our low-protein rations may have been excessive in relation to the capacity of channel catfish to utilize carbohydrate efficiently. Some authors (Phillips *et al.*, 1940:24-25, 1963:39-44; McLaren *et al.*, 1946:440) have concluded that trout have limited tolerance for carbohydrate, because their fish grew poorly and/or had liver-abnormalities when fed diets high in carbohydrates. In contrast, Buhler and Halver (1961:307) and DeLong *et al.* (1958) found that chinook salmon use carbohydrates at levels of 48 to 63 per cent of the diet without ill effects or decrease in growth. Nail (*loc. cit.*) reported that carbohydrate-levels of at least 18.6 per cent are beneficial to channel catfish and suggested that higher levels probably can be utilized efficiently by that species. The carbohydrate-levels in diets that we

used were approximately 30, 50, and 70 per cent in the rations containing 60, 40, and 20 per cent protein, respectively.

Large variations in the digestion- and absorption-rates of different forms of carbohydrate were reported by Tunison *et al.* (1943:10); on the average, 75 per cent of total sucrose in rations was absorbed by brook trout, but only 65 per cent of total dextrin and 40 per cent of total starch were utilized. Therefore, if high carbohydrate-levels are harmful rather than beneficial to catfish, the deleterious effect of diets containing starch might be less than that of diets containing sucrose, accounting for the better gains by fish receiving high levels of starch than by those receiving high levels of sucrose in our tests (Figure 2).

In an unrelated set of experiments, we have noted that the degree of enlargement and vacuolar degeneration in livers of fed channel catfish varied inversely with the protein-level in their rations (hence tissue-damage correlated with carbohydrate-content). These results were obtained with pondfish fed pelleted rations composed of commercial foodstuffs, and will be reported elsewhere by C. E. Judd and Cross; but, the findings seem pertinent to the above discussion in suggesting that a high intake of digestible carbohydrate may be detrimental to channel catfish.

GROWTH ON FEEDS CONTAINING DIFFERENT AMOUNTS OF PROTEIN

Channel catfish are omnivorous, at least in some degree (Davis, 1959:6). In many natural waters insects are the primary food of channel catfish (Bailey and Harrison, 1948:125-130), but the variety of items other than insects that have been found in stomachs of channel catfish attests that they are opportunistic in their feeding habits. Perhaps because of this lack of selectivity, channel catfish respond well to supplemental feeding (Swingle, 1959; Tiemeier, 1962), making it possible to increase pond-production by several hundred pounds per acre. Although several investigators (Swingle, 1957, 1959; Tiemeier, 1957, 1962, 1965; Nail, 1965) reported the results of supplemental feeding, relatively little has been published concerning the effects of supplemental feeds containing various levels of protein.

In order to test the response by channel catfish stocked in earthen ponds, to feeds containing different levels of protein, studies were made in 1961 and 1962 using supplemental feeds having 20, 30, 40 and 50 per cent protein (see Table 5 for composition of feeds).

Table 5.—Composition of Pelleted Feeds Used in Ponds in 1961 and 1962 (Expressed in Per Cent).

Source	Per cent protein			
	20	30†	40†	50
Blood meal	1.5	3.5	5.5	7.9
Fish meal	7.4	17.25	27.2	39.45
Soybean meal	7.4	17.25	27.2	39.45
Corn, ground yellow	32.5	23.7	13.85	2.8
Wheat bran††	44.8	31.8	19.8	3.9
Brewer's dried yeast	4.9	4.9	4.9	4.9
Salt	1.5	1.5	1.5	1.5
Vitamin A concentrate‡	0.1	0.1	0.1	0.1

† In 1961, 30 and 40 per cent protein-feeds were formed by mixing the 20 and 50 per cent protein-feeds in the desired proportions.

†† Wheat bran used in 1961, wheat brown shorts used in 1962.

‡ Vitamin A Concentrate added only in 1962.

The growth-rates of catfish receiving these feeds are represented by the lower set of 4 lines in Figure 3, for biweekly intervals in the summer of 1961. The weight of fish in each pond was the same when the ponds were filled and stocked on May 13-15, 1961. Variation in growth associated with the different feeds was evident when the fish were checked in June. The estimated weights of catfish fed 20, 30, 40 and 50 per cent protein-feeds were, respectively, 73, 90, 121, and 79 lbs./A on June 12, and 93, 107, 141, and 127 lbs./A on June 26. On these two dates, there seemed to be a correlation between growth-rate of the fish and the protein-level of the feed. Thereafter, the standing crops fluctuated but growth by fish receiving 30, 40, or 50 per cent protein differed only slightly through August 8. Growth on the 20 per cent protein-feed was consistently lower than that on the other rations during this period. The standing crops on August 8, 1961, of fish receiving 20, 30, 40 and 50 per cent protein feeds were 315, 467, 455 and 433 lbs./A respectively. Subsequently, greater divergence in growth-rates occurred. Yields when the ponds were drained in November were 550, 703, 783, and 624 lbs./A, in order of increasing protein-level in the feed.

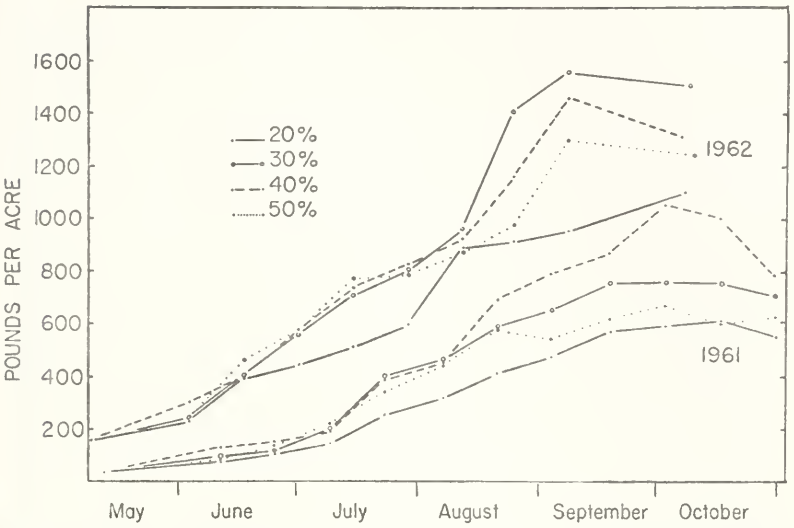

FIG. 3. Standing Crops (in Pounds Per Acre) of Channel Catfish that Received Feeds Containing Different Amounts of Protein, in Open Ponds in 1961 (Lower Set of Four Lines) and 1962 (Upper Set of Four Lines).

An analysis of variance, based on individual weights of 25 fish from each pond when drained in November, gave the following results:

Source of variation	Degrees of freedom	Mean square	F
Among Feeds	3	0.0353	3.53 *
Within Feeds	96	0.0105	

Variation among feeds was significant at the 95 per cent probability-level. In order to determine where the differences lay, a Duncan's Multiple Range test was applied (Steel and Torrie, 1960:107-109), using the mean weight obtained on each feed. The results are as follows:

Feed (% Protein)	20	50	30	40
Mean Weight (Pounds)	0.24	0.27	0.30	0.33

Weights underlined are not significantly different at the 95 per cent level of probability. Note that 50 per cent protein-ration is listed out of sequence; the groups are arranged in increasing order of weights of fish. Factors other than protein-level are thought to have influenced the results of this experiment, and are discussed on page 240.

The 30 per cent protein-ration was used in a second pond in 1961. (This pond will henceforth be designated Pond 30B and the pond discussed above, where the same 30 per cent protein-ration was used at the same daily rate, will be designated Pond 30A.) Pond 30B was a holding-pond that contained 20,000 fingerling catfish overwinter, whereas the other ponds were dry in that season. Pond 30B was stocked two weeks later with smaller fish than those stocked in the other ponds. Thus the experimental conditions in Pond 30B did not duplicate those in Pond 30A. The growth-rates of fish in the two ponds receiving 30 per cent protein feeds are diagrammed in Figure 4. Throughout late spring and summer, the initial difference in size of the two groups of fish persisted, but the rates of growth by fish in both ponds seemed similar. Growth by catfish in Pond 30B continued later into fall than did growth of fish in Pond

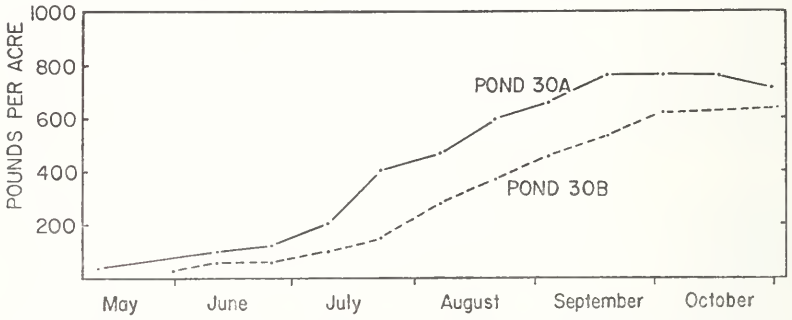

Fig. 4. Standing Crops (in Pounds Per Acre) of Channel Catfish in Two Ponds Where the Same Feed, Containing 30 Per Cent Protein, Was Used in 1961.

30A, where no gains in weight were recorded after September 21. Thus the fish in Pond 30B almost overcame their initial deficit and attained sizes almost as large as those of fish in Pond 30A. Values of "t" contrasting these two ponds on three dates, based on individual lengths of fish were: June 26—8.75 **, October 4—2.807 *, and November 4—2.025 n.s. An analysis of variance based on individual weights at the time of draining (November 4) was also non-significant ($F = 2.02$, d.f. $= 1/48$). Although our analysis detected no significant difference in the average size of the fish in the two ponds (as compared to the variability among fish within each pond), the actual yield was 13 per cent (81 pounds per acre) higher in Pond 30A than in 30B. Values of "t" obtained in a comparison of the yield of Pond 30B with yields of other ponds used in 1961 are given below, based on weights of individual fish in each pond:

Feed Used (% Protein) ...	20	30A	40	50
Yield (Pounds Per Acre) ..	550	703	783	624
30B, 622 pounds	1.59 n.s.	–1.69 n.s.	–3.27 **	–0.13 n.s.

The poundage of fish obtained from Pond 30B was significantly lower than that obtained in the pond where fish received a 40 per cent protein ration; differences in yields between Pond 30B and the other ponds were not significant. In contrast, the yield in Pond 30A was significantly higher than that in the pond where a 20 per cent protein-ration was used, and was not significantly lower than that in the pond where a 40 per cent protein ration was fed. In both ponds where 30 per cent protein-feed was used, absolute yields were higher (by 72 and 153 lbs./A) than those obtained from the 20 per cent protein-feed.

Experimental feeding of rations containing different levels of protein were repeated in 1962 (Table 5). The patterns of growth in the different ponds are shown by the upper set of four lines in Figure 3. Fish receiving the 20 per cent ration grew slowly in late June and early July, but on August 13, our samples indicated that these fish had attained weights approximating those in the other ponds. The estimated standing crops of fish on three dates in summer are given below:

Feed used (% protein)	June 18	July 16	August 13
20	390	520	890
30	388	705	964
40	394	734	922
50	457	770	882

Through August 13, differences in weight-gain on 30, 40, and 50 per cent protein were small. Subsequently, differences in growth-rates increased. The fish fed the 30 per cent protein-ration had the highest standing crop on August 13, and maintained the fastest growth-rate thereafter. Drainage of the ponds in October yielded poundages of fish on the 20, 30, 40, and 50 per cent protein-rations respectively, as follows: 1103, 1515, 1314, and 1245 pounds per acre. An analysis of variance based on mean weights of fish in 14 subsamples from each pond gave the following results:

Source of variation	Degrees of freedom	Mean square	F
Among Feeds	3	0.113	20.46 **
Within Feeds	52	0.00552	

Variation among feeds was highly significant. A Duncan's Multiple Range test, based on the average weight of the fish receiving each feed, indicated highly significant differences ($P = .99$) in the weights obtained on all feeds, with one exception—the results on

the 40 and 50 per cent protein rations were not significantly different ($P \neq .95$).

Production on Same Ration in Different Years

Productions obtained in 1962 were much higher than those obtained on the same feeds in 1961 (Figure 3). The highest standing crop present at any time in 1961 was lower than the lowest standing crop on the same date in 1962. An analysis of variance indicated highly significant differences between gains made by fingerling catfish on the same experimental rations, in 1961 and 1962:

Source of variation	Degrees of freedom	Mean square	F
Between years	1	791,911	97.1 **
Among Feeds	3	31,310	3.84 n.s.
Discrepance	3	8,156	

Thus, factors other than the type of feed affected the standing crops obtained in these two years. The same stocking-rates were used in both years, but the fingerling catfish stocked in 1962 were larger than those stocked in 1961; not until early July did the 1961-fish attain a size equal to that of the 1962-fish when the latter were stocked in May, 1962. The fish in 1962 maintained their size-advantage throughout the growing season. Factors other than protein-level and initial size of fish (for example, variation in weather and differences in water-chemistry) may have contributed to the differences obtained in the two years; some of these factors will be discussed later.

Growth by Subadults Fed Experimental Rations in a Second Year

In order to test the effect of different protein-rations in two growing seasons, each of two ponds was stocked 1962 with an equal number of subadult catfish that had received 40 per cent protein and 20 per cent protein in 1961. The adipose fin was clipped on the fish that had received the 40 per cent protein-feed, for identification. In 1962, the 20 per cent ration was used in one pond, and the 40 per cent ration in the other. Thus, half of the fish in each pond received the same feed, and half received a different protein-level than that fed to them in the previous year. Some fish (an equal number from each group) were removed for observation during the summer. The poundages of fish at the time of stocking (April 17) and draining (October 2-4, 1962) are presented in Table 6.

An analysis of variance was performed based on random subsamples of all fish taken at the time of draining:

Source of variation	Degrees of freedom	Mean square	F
Between Ponds	1	0.019	0.359 n.s.
Between Groups			
Within Each Pond	1	0.2173	7.148 *
Interaction	1	0.0469	1.543 n.s.
Error	28	0.0304	

TABLE 6.—GAINS (IN POUNDS) MADE BY CATFISH RECEIVING EXPERIMENTAL RATIONS OVER A TWO-YEAR PERIOD.

Feed used (% protein)		Pond number (1962)	Poundage stocked per acre in 1962	Yield (lbs./A) in 1962	Gain (lbs./A) in 1962	Proportional gain (in per cent)
1961	1962					
20	20	4	187	658	471	252
40	20	4	260	682	422	162
			447	1,340	893	
20	40	3	166	617	451	271
40	40	3	262	784	522	200
			428	1,401	973	

The yields of the two ponds in 1962 did not differ significantly; therefore, the advantage of a 40 per cent protein-ration over a 20-per cent protein-ration seemed far less among subadult catfish (0.20-1.40 pounds) than among fingerling catfish. The fish that were fed 40 per cent protein as fingerlings were larger when stocked in the two ponds than were the fish previously fed 20 per cent protein; the significant difference persisted to the time when the two ponds were drained in 1962. The two groups of fish that gained the most weight in 1962 were those that received the same ration in both years—whether their ration contained 40 per cent protein or 20 per cent protein. This result is consistent with the findings by Shell (1963), who reported that growth-rates of channel catfish decreased temporarily after a change in the protein-level of their feed —whether protein was increased or decreased. However, the period of feeding in our experiments was much longer than the term of the residual effect reported by Shell.

Further interpretation of our results is complicated by differences in size among the four groups of fish when they were stocked in 1962, relative to known variation in the capacity for growth by fish at different stages in their life-histories. As a general rule, a large fish can (potentially) gain more weight in a brief interval

than can a small fish; but, the gain made by the small fish generally is higher proportional to its initial weight than that made by the large fish. From the standpoint of this rule, the order of absolute gains by the four groups of fish (from largest to smallest) should have been as follows if the protein-level in their feed in 1962 were *not* a factor: group 40-40, group 40-20, group 20-20, group 20-40. The expected order of proportional gains, again from greatest to least, should have been as follows for fish on the four rations: 20-40, 20-20, 40-20, 40-40. The absolute and the proportional gains actually made by our fish fall in the expected order, with the exception of the group fed 40 per cent protein in 1961 and 20 per cent protein in 1962. That group gained less than expected, both proportionally and absolutely, in 1962 (Table 6).

Seemingly, the advantage of 40 per cent protein over 20 per cent protein in feeding fingerling fish, which increased their weight 20 or more times during one growing season, is much less pronounced in feeding larger (subadult) catfish, which increased their weight less than threefold in one season.

Feeding Different Amounts of Protein in Same Pond

On August 16, 1962, each of five sections in the two ponds subdivided by screens (Figure 1) was stocked with 40 channel catfish. The fish stocked had been held together in another pond for several months previously. A 20, 30, 40, or 50 per cent protein-ration was fed to fish in one section of each pond; the "end" section was used as a "control" where fish received no supplemental feed. Selection of the feed used in each section was by blind drawings. Eight ounces of feed were fed daily to each group of fish; therefore the feeding-rate, relative to fish-weight, declined during the course of the experiment (5 per cent of body-weight per day on August 16; 1.8 to 2.3 per cent of body-weight on October 18-19). The experiment continued 64-65 days, until the ponds were drained on October 18-19, 1962. The results are shown in Table 7 and Figure 5.

Experimental feeding obviously increased production, because the fish that were fed gained 12 to 17 times as much as the unfed "control" fish. An analysis of variance indicated that gains in Pond 10 did not differ significantly from gains in Pond 11. Absolute gains made on each ration (Table 7) correlated directly with the amount of protein in the rations, and differed significantly ($P = .95$):

Source of variation	Degrees of freedom	Mean square	F
Among feeds	3	9.3992	14.352 *
Between ponds	1	.6786	1.036 n.s.
Remainder	3	.6549	

TABLE 7.—GAINS MADE BY YEARLING CHANNEL CATFISH ON EXPERIMENTAL RATIONS, IN SUBDIVIDED PONDS IN 1962.

Feed used (% protein)	Pond number	Section number	Pounds stocked	Pounds harvested	Pounds gained
No feed	10	end	9.49	9.69	0.20
	11	end	9.54	11.44	1.90
					2.10
20	10	D	9.65	21.65	11.91
	11	B	9.72	22.44	12.72
					24.63
30	10	B	9.81	25.13	15.32
	11	A	9.79	24.38	14.59
					29.91
40	10	A	9.77	25.38	15.61
	11	C	9.57	27.19	17.62
					33.23
50	10	C	9.68	26.69	17 01
	11	D	9.75	27.00	17.25
					34.26

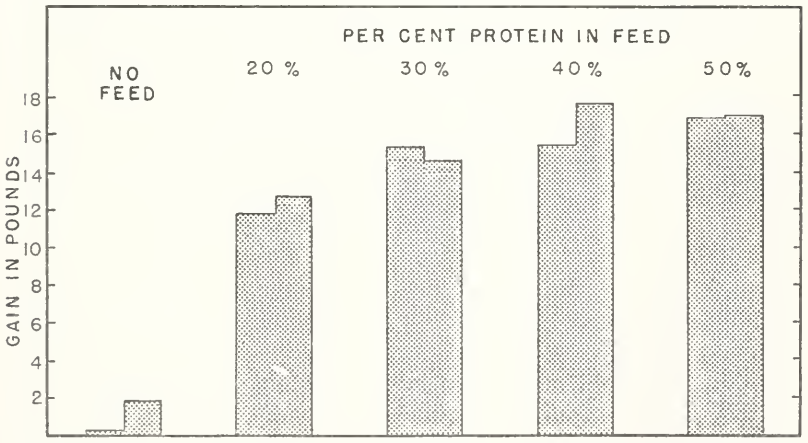

FIG. 5. Gains in Pounds by Channel Catfish in Subdivided Ponds, on Feeds Containing Different Amounts of Protein, August 16-October 18, 1962.

Summary of Effects of Various Levels of Protein on Growth

The cumulative results of experiments involving variable protein-levels cannot be summarized in terms of absolute gains made by

fish on each ration, because of other variables such as 1) differences in size of the open ponds and the sections of the subdivided ponds, 2) differences in the number and size of fish stocked therein, and 3) differences between years. But results can be summarized if gains by the catfish are expressed on a relative basis, using the following procedure. The results are treated as independent sets, depending on the year of study and whether the experimental units were open ponds or sections of subdivided ponds. Within each set of comparable experiments, the weight gained on each of the four feeds is converted to a percentage of the total gain in weight by all fish on all rations in that set. For example, the gain of 522 pounds per acre by fish that were fed a 20 per cent protein-feed in an open pond in 1961 represented 20.5 per cent of the total gain (2660 pounds) made by fish on all four feeds in open ponds in 1961. Relative gains on each protein-level, calculated in this manner, are shown in Figure 6.

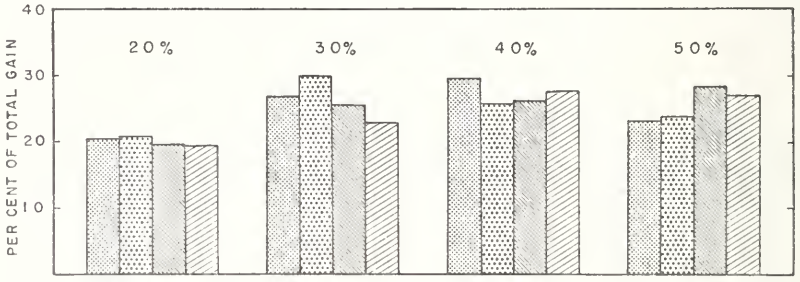

Fig. 6. Relative Gains Made by Channel Catfish on Feeds Containing Different Amounts of Protein (20 to 50 Per Cent). Height of Bar Indicates the Percentage of Total Gain Made by Fish on All Rations, under Similar Experimental Conditions. Within Each Set of Four Bars, Bar 1 (left) = Open Ponds in 1961; Bar 2 = Open Ponds in 1962; Bar 3 = Subdivisions of Pond 10 in 1962; Bar 4 = Subdivisions of Pond 11 in 1962.

Gains made on the 20 per cent protein-feed were consistently less than those on feeds containing higher levels of protein, but were much greater than gains where no feed was used. Thus feeds containing 20 per cent protein will produce satisfactory yields of channel catfish in ponds. Gains on the 30 per cent ration were usually as good as or better than gains on 40 per cent and 50 per cent protein.

Feeds containing high protein-levels cost more than those containing less protein. Our 30 per cent feed cost approximately 4.5 cents per pound, whereas the 20 per cent feed cost about 3.5 cents per pound, for a saving of 22 per cent. In four comparable sets of

experiments, our fish-production on the 20 per cent protein-feed was 17 per cent to 29 per cent lower (average 23 per cent lower) than on the 30 per cent ration. Thus, the increased cost of the feed containing 30 per cent protein was nearly balanced by increased yields. Taking account of other factors such as labor-costs and the length of time required to raise the fish to the desired size (with attendant risk of mortality), we conclude that the 30 per cent protein-feed was the best of those that we used.

EFFECT OF SUPPLEMENTAL FEEDING ON CONDITION

Does supplemental feeding of channel catfish merely increase their rate of growth, or is the condition (or relative plumpness) of the catfish altered also?

Length-weight relationships were calculated by the procedure of Swingle (1964) for 141 groups of catfish (864 individuals) from various reservoirs in Kansas (Davis, 1959:16-17), and for 338 groups of channel catfish (7,791 individuals) that had received supplemental feeds in our experimental ponds. The length-weight curve was calculated using the following formula:

$$W = a_L{}^b$$

where W is the weight in pounds, a is the Y-intercept, b is the slope and L is the length in inches. The correlation coefficient for each curve exceeded 0.99. For fish that received supplemental feed, the average weight at 0.2-inch intervals of length is given in Table 8.

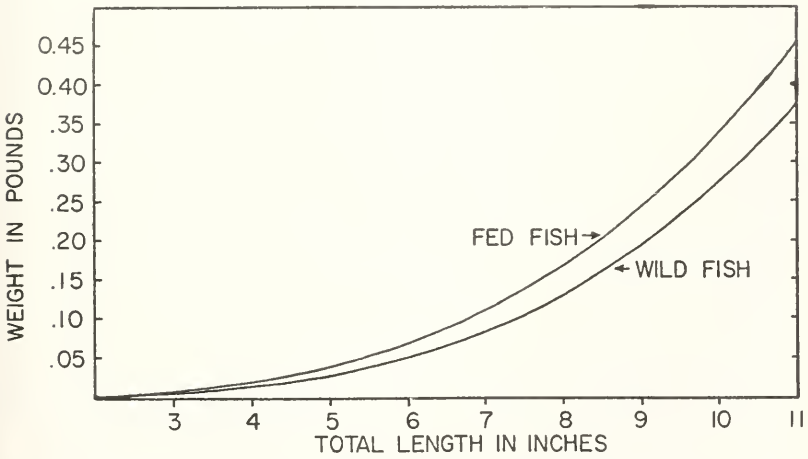

FIG. 7A. Length-weight Relationships of Channel Catfish That Have Been Fed Intensively in Ponds, and of Wild Channel Catfish from Impoundments in Kansas.

The length-weight curve of channel catfish from Oklahoma (Finnell and Jenkins, 1954) closely approximates that of catfish from reservoirs in Kansas (Figure 7). At any given length, catfish that were fed in our experimental ponds were slightly heavier than "wild" fish from either state. The slope of the length-weight curve (the exponent b, above) for catfish that received supplemental feeds, for catfish from reservoirs in Kansas, and for catfish from Oklahoma, was 3.099, 3.304, and 3.407, respectively. Thus the weight of channel catfish increases by a power slightly greater than the cube of its length. Catfish that were fed most closely approached the theoretical cubic relationship that is often used in obtaining indices of plumpness of fish (see below).

In order to express the relative plumpness of a fish as a numerical value, the ratio of volume (weight) to surface (length) is calculated. This value is known as the "condition index"; a fat fish will

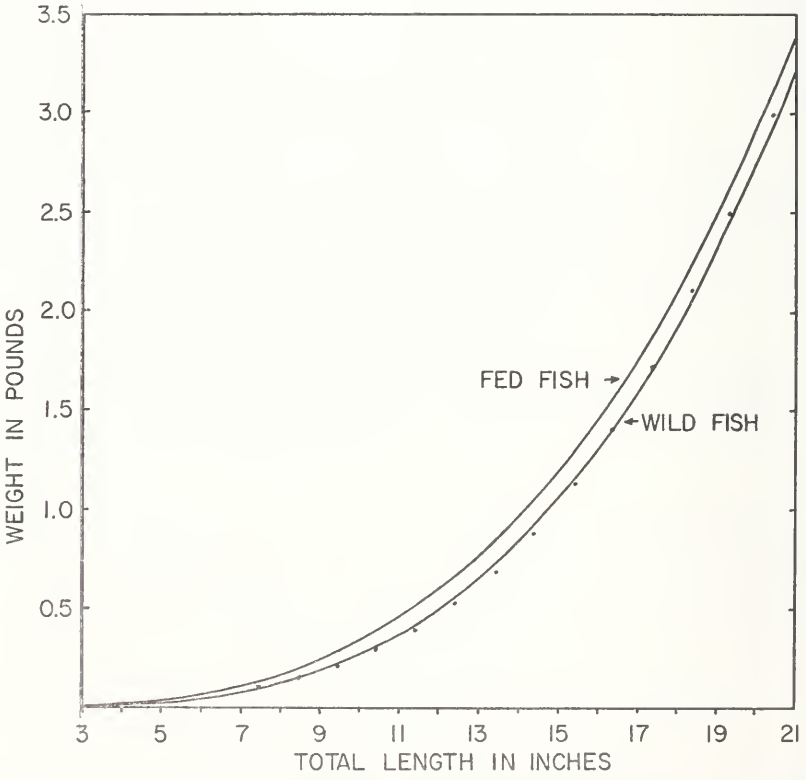

Fig. 7B. Length-weight Relationships of Channel Catfish That Have Been Fed Intensively in Ponds and of Wild Channel Catfish from Impoundments in Kansas. Dots Indicate Values for Wild Channel Catfish from Oklahoma.

TABLE 8.—LENGTH-WEIGHT RELATIONSHIP OF CHANNEL CATFISH THAT RECEIVED SUPPLEMENTAL FEEDS.

Length (inches)	Weight (pounds)	Number per pound	Length (inches)	Weight (pounds)
3.0	0.008	125	14.2	1.006
3.2	0.010	100	14.4	1.050
3.4	0.012	83.3	14.6	1.096
3.6	0.014	71.4	14.8	1.143
3.8	0.017	58.8	15.0	1.192
4.0	0.020	50	15.2	1.242
4.2	0.023	43.3	15.4	1.293
4.4	0.027	37.3	15.6	1.346
4.6	0.031	32.2	15.8	1.400
4.8	0.035	28.5	16.0	1.456
5.0	0.040	25	16.2	1.513
5.2	0.045	22.2	16 4	1.571
5.4	0.050	20	16.6	1.631
5.6	0.056	17.7	16.8	1.693
5.8	0.063	15.8	17.0	1.756
6.0	0.070	14.2	17.2	1.821
6.2	0.077	12.9	17.4	1.887
6.4	0.085	11.7	17.6	1.956
6.6	0.094	10.6	17.8	2.025
6.8	0.103	9.7	18.0	2.097
7.0	0.112	8.9	18.2	2.170
7.2	0.123	8.1	18.4	2.244
7.4	0.133	7.5	18.6	2.321
7.6	0.145	6.2	18.8	2 400
7.8	0.157	6.04	19.0	2.479
8.0	0.170	5.8	19.2	2.561
8.2	0.183	5.4	19.4	2.644
8.4	0.198	5.05	19.6	2.730
8.6	0 213	4.7	19.8	2.817
8.8	0.228	4.3	20.0	2.906
9.0	0.245	4.08	20.2	2.997
9.2	0.262	3 8	20.4	3.090
9.4	0.280	3.5	20.6	3.185
9.6	0.299	3.3	20.8	3.281
9.8	0.319	3.1	21.0	3.380
10.0	0.339	2.9	21 2	3.481
10.2	0.360	2.7	21.4	3.584
10.4	0.383	2.6	21.6	3.689
10.6	0.406	2.4	21.8	3.795
10.8	0.431	2.3	22.0	3.904
11.0	0.456	2.2	22.2	4.015
11.2	0.482	2.07	22.4	4.129
11.4	0.509	1.9	22.6	4 244
11.6	0.537	1.8	22.8	4.361
11.8	0.567	1.7	23.0	4.481
12 0	0.597	1.6	23.2	4.603
12.2	0.628	1.59	23.4	4.727
12.4	0.661	1.5	23.6	4.853
12.6	0 694	1.41	23.8	4.982
12.8	0.729	1.37	24.0	5.112
13.0	0.765	1.3	24.2	5.246
13.2	0.802	1.2	24.4	5 381
13.4	0.840	1.18	24.6	5.519
13.6	0.880	1.1	24.8	5.660
13.8	0.920	1.08	25.0	5.802
14.0	0.962	1 04		

have a higher condition index than a thin fish of the same species and length (Bennett, 1962:76). The weight of a fish varies with the cube of its length provided the shape and specific gravity remain the same; any change in the shape or relative plumpness of a fish will cause a change in the value of C in the formula:

$$C = \frac{W\ 10^5}{L^3}$$

(Carlander, 1950:8). In our study the value of "C" was calculated from total lengths (L) in inches and weights (W) in pounds. For convenience, the weight is raised to a power sufficient to provide for two digits to the left of the decimal.

The condition indices of fish that received experimental feeds in our ponds in 1961 and 1962 are shown in Figure 8; the rates of growth by the same fish were presented in Figure 3. Also shown in Figure 8 are average condition indices of wild channel catfish, from reservoirs in Kansas, at sizes identical to those of the fed fish in biweekly samples from our ponds.

Throughout late spring and summer, the condition index of the fed fish was higher than that of wild fish of comparable size (the "fed" fish had been fed for some time before their condition index was calculated for the first time in May). But, the condition index of wild fish increases as their lengths increase, whereas no such

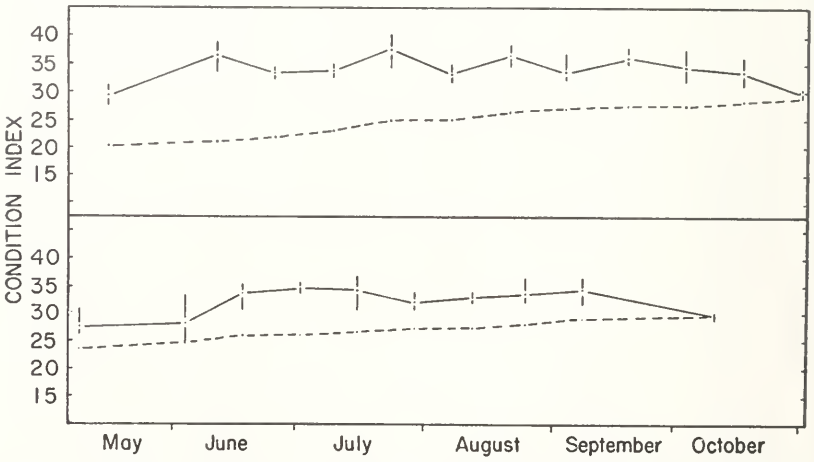

Fig. 8. Values of Condition Index Among Fish Being Fed in Ponds (Solid Lines) Compared with Average Condition Index of Wild Channel Catfish of Similar Size (Dash-lines). Vertical Bars Indicate Range of Values for Individual Fish, on Each Date when Samples Were Obtained. Upper Part of Graph Represents Data Obtained from All Ponds in 1961, Lower Part, Data Obtained in 1962.

trend existed among the fish being fed in our ponds (Figures 3 and 8). Therefore, the condition *advantage* of the fed fish diminished as they grew larger, and as their standing crops increased in the ponds. Additionally, the condition index of the fed fish actually decreased in late summer. When the ponds were drained in October of 1961 and 1962, the condition indices of the fed fish approximated those of wild fish of similar size (Figure 8). Samples of fish that were weighed biweekly in 1961 and 1962 indicated that the catfish lost weight in late summer and early autumn in most ponds (Figure 3). The concomitant decrease in condition index adds evidence that a decline in standing crops actually occurred (was not an artifact attributable solely to sampling-error). Presumably, the fish ceased to grow and utilized fat for energy, causing loss in their weight and reduction in their condition index.

To obtain maximum production from ponds, the fish should be harvested prior to any loss of condition. The period in which weight-loss occurs may vary with the prevalent temperature and the standing crop of fish being held in a pond. In our ponds, such losses usually have occurred in late September or October.

EFFECT OF DAILY FEEDING-RATE ON PRODUCTION

In order to obtain the most efficient utilization of supplemental feeds by channel catfish, a satisfactory feeding-rate, as well as a satisfactory kind of feed, must be determined. In ponds used for commercial production in Alabama, Swingle (1959:66) reported feeding at rates principally between two and five per cent of the weight of fish in the ponds; the fish were fed six days each week. He indicated that the maximum amount that could be fed without mortality due to oxygen-deficiency was 30 pounds per acre per day. Snow (1962:114) fed channel catfish fry at an initial rate of 5 per cent of body-weight per day, but the rate he used decreased to about one percent by the time his ponds were drained after 109-136 days of feeding. Snow judged a rate of 20 pounds per acre per day to be about as high a feeding-rate as could be used safely for a sustained period.

In our experiments, 35 fingerling catfish were stocked on July 5, 1963, in each section of the subdivided ponds, and were fed at various rates from July 8 to October 10 (Table 9).

The feeding-rates cited are maximal rates, restored after biweekly samples of fish from each section permitted recalculation of the rates, based on gains made by the fish in each two-week interval. Average feeding rates would be less than those shown in Table 9.

TABLE 9.—FEEDING-RATES (PER CENT OF BODY WEIGHT PER DAY) AND POUNDAGE OF FISH STOCKED, IN SECTIONS OF SUBDIVIDED PONDS, 1963.

Feeding-rate (% of body weight)	Section	Total poundage of fish stocked	
		Pond 10	Pond 11
None	E	3.49	
	E		3.57
2	A	3.48	
	D		3.47
3.5	B	3.43	
	C		3.39
5	C	3.37	
	B		3.34
7	D	3.50	
	A		3.44

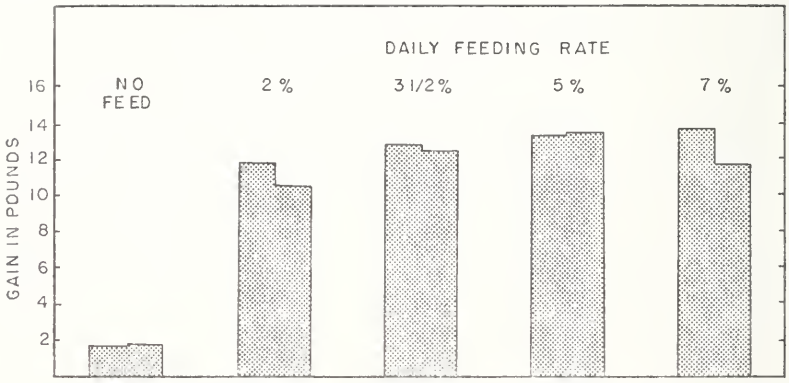

FIG. 9. Gains in Pounds Made by Channel Catfish that Were Fed at Different Daily Rates in Subdivided Ponds, July 8 to October 10, 1963. Feed Used Contained 30 Per Cent Protein.

The experiment was terminated after 95 days (ponds drained October 10-11, 1963). The gains made on each feeding-rate are presented in Figure 9. An analysis of variance based on large samples from each of the sections (including the "control" group) indicated no significant difference between ponds, but a highly significant difference among gains by the five groups of fish within each pond:

Source of variation	Degrees of freedom	Mean square
Between Ponds	1	0.00037 n.s.
Among Feeding Rates	4	0.596 **
Interaction	4	0.033 n.s.
Remainder	140	0.0226

An analysis of variance performed on individual weights, from sections where fish were fed (excluding "controls"), detected no significant differences among gains made on the four feeding-rates.

Source of variation	Degrees of freedom	Mean square
Among Rates	7	0.0264 n.s.
Within Ponds	112	0.0276

Thus, where supplemental feeds were used, the weights of fish were significantly higher than weights of fish that received no supplemental feed. Although higher feeding-rates generally resulted in higher yields (Figure 9) these differences were non-significant ($P \neq .95$).

The efficiency of different feeding-rates can be measured by calculating the conversion of feed to flesh. The conversion-factors (feed used divided by weight gained by fish) of the fish that were fed at different daily rates are given in Table 10. For each period in summer, less efficient conversions usually were associated with higher feeding rates. Conversion-values for the entire summer for each feeding-rate were as follows: 2 per cent—1.25; 3.5 per cent—2.20; 5 per cent—3.20; 7 per cent—4.28.

Different feeding-rates have been used in various experiments in open ponds; the conversion-factors and the productions obtained are presented in Table 11.

As one might expect, the efficiency of conversion of supplemental feed to flesh decreases as the feeding-rate increases. Thus the lowest feeding rate (2 per cent) resulted in the best conversion, while the highest rate (7 per cent) provided the least efficient conversion.

The productions obtained are not directly correlated with the feeding-rates. Our results agree with findings by Swingle (1959: 66), who reported inefficient conversions when feeding-rates higher than five per cent were used. Swingle reported also a decrease in growth-rate associated with a decrease in feeding-rates from five to one per cent. Similar results were obtained in our subdivided ponds (see Figure 9). However, in the open ponds discussed above, productions were highest where the feeding-rate was 3 per cent. Productions obtained with feeding-rates of 7 per cent were generally lower than those obtained on rates of 2.5, 3, and 3-5 per cent. The low production obtained with the seven per cent feeding-rate (as well as the poor conversions) may be due to excessive feed that fouled the water. But, in four of the five ponds where fish were fed at the rate of seven per cent, diurnal oxygen-levels were consistently higher than 4 ppm throughout the summer, and poor growth did not seem to be caused by oxygen-depletion.

TABLE 10.—PERIODIC GAINS AND CONVERSION-VALUES (FEED USED/WEIGHT GAINED BY FISH) OF FINGERLING CATFISH THAT WERE FED DIFFERENT AMOUNTS OF A PELLETED RATION CONTAINING 30 PER CENT PROTEIN IN SUBDIVIDED PONDS IN 1963.

PERIOD	POND	Daily feeding rate											
		2 per cent			3½ per cent			5 per cent			7 per cent		
		Feed lbs.	Gain lbs.	Conv.	Feed lbs.	Gain lbs.	Conv.	Feed lbs.	Gain lbs.	Conv.	Feed lbs.	Gain lbs.	Conv.
8 July–21 July.....	10	0.86	0.76	1.13	1.76	0.63	2.79	2.62	1.11	2.36	3.48	0.77	4.52
	11	0.86	-0.14	Neg.†	1.76	0.64	2.75	2.62	1.18	2.22	3.48	0.62	5.61
22 July–4 August.....	10	1.19	1.59	0.75	1.99	1.59	1.25	3.14	2.04	1.54	4.18	1.68	2.49
	11	0.93	1.52	1.30†	1.97	2.05	0.96	3.18	2.67	1.19	3.98	2.57	1.55
5 August–18 August...	10	1.63	0.82	1.99	2.77	1.70	1.63	4.56	0.83	5.49	5.83	2.27	2.57
	11	1.36	1.54	0.88	3.08	2.50	1.23	5.03	4.17	1.21	6.50	0.67	9.70
19 August–1 Sept.....	10	1.86	2.52	0.74	3.60	3.61	1.00	5.15	3.71	1.39	8.06	2.42	3.33
	11	1.79	2.71	0.66	4.20	2.62	1.60	6.08	5.28	1.15	7.15	4.29	1.67
2 Sept.–15 Sept.....	10	2.56	3.60	0.71	5.37	3.09	1.74	7.74	2.59	2.99	10.42	2.70	3.86
	11	2.56	3.33	0.77	5.49	2.84	1.93	9.78	1.92	5.09	11.35	1.08	10.51
16 Sept.–10–11 Oct....	10	6.13	2.49	2.46	11.79	2.17	5.43	16.39	2.96	5 54	22.41	3.82	5.87
	11	5.97	1.48	4.03	11.79	1.87	6.30	19.08	0.93	20.42	21.30	2.38	8.95
Totals (entire term) 8 July–10–11 October..	10	14.24	11.78	1.21	27.27	12.79	2.13	39.60	13.24	2.69	54.39	13.66	3.98
	11	13.47	10.44	1.29	28.29	12.52	2.26	45.77	13.48	3.40	53.77	11.61	4.63
Totals (both ponds)....	.....	27.71	22.22	1.25	55.56	25.31	2.20	85.37	26.72	3.20	108.16	25.27	4.28

† Weight-loss by fish prevented calculation of a conversion-factor in the initial period. The factor tabulated for the second period (22 July) is based on feed used and gains made during both periods (cumulative).

TABLE 11.—PRODUCTION (POUNDS PER ACRE) AND CONVERSION (FEED USED DIVIDED BY WEIGHT GAINED BY FISH) USING VARIOUS FEEDING-RATES IN OPEN PONDS. EXPERIMENTS WERE CONDUCTED IN DIFFERENT YEARS, AND DIFFERENT AGE GROUPS ARE INVOLVED. FEEDING RATES LISTED ARE INITIAL RATES THAT WERE ADJUSTED PERIODICALLY, AND ARE THUS THE MAXIMAL FEEDING RATE DURING THE PERIOD RATHER THAN THE AVERAGE RATE.

2.5%		3%		3-5%†		7%	
Production	Conversion	Production	Conversion	Production	Conversion	Production	Conversion
691	1.94	1835	2.12	1054	3.35	522	6.50
755	2.00	1936	2.07	1217	3.61	596	6.79
721	2.10	1224	3.74‡	1303	3.52	610	5.28
1359	1.54	947	4.61‡	1504	3.17	675	6.67
.....	.....	.....	.....	.....	.....	751	6.67

† 5%, May 21-August 27; 4%, August 28-September 10; 3%, September 11-October 8-11.

‡ Subadult catfish; all other groups were fingerlings.

Whatever the reason, the poor conversion-values and poor production obtained with the seven per cent rate indicate that feeding at this level is uneconomical. The productions that we obtained on the 3 per cent feeding-rate demonstrate that this rate is sufficient to produce crops that approach the carrying capacity of our ponds.

The subdivided ponds were each stocked with 1620 fish per acre in 1964. Both ponds were fed at the rate of 3 per cent of fish-weight per day from May 11 to August 24, 1964. On the latter date the estimated poundages of fish in the two ponds were nearly identical (1201.0 lbs./A in Pond 10; 1208.2 lbs./A in Pond 11). For the remainder of the season (August 25 to October 4) the feeding-rate in Pond 11 was reduced from 3 per cent to 2 per cent. The feeding-rate in Pond 10 remained at 3 per cent. The yields obtained on October 8-9 in Ponds 10 and 11 were 1316.9 and 1461.2 lbs./A, respectively (see Table 15). In this instance, a late-season reduction in the daily feeding rate proved advantageous.

Limitation of the feeding-rate to an amount less than 30 lbs./A/day (pounds per acre per day) as suggested by Swingle (1959:66) does not seem necessary. In one pond in which a production of 1936 pounds per acre was obtained (Table 11), our feeding rate of three per cent sometimes amounted to more than 45 lbs./A/day, and did not create unfavorable conditions for growth by fish in the

pond. Use of large amounts of feed requires a full knowledge of the number and weight of fish in the pond, and of prevalent water-conditions, but may result in increased production.

Experiments in subdivided and open ponds indicate that feeding-rates of two to three per cent of fish-weight per day probably are the most favorable rates for economical production of channel catfish.

EFFECT OF STOCKING-RATE ON PRODUCTION

Various studies (Swingle, 1957, 1959; Hickling, 1962:237-245; Tiemeier, 1957; and our own results) indicate that the number of fish stocked influences production. We stocked fingerling catfish (average length 3.1 inches, average weight 0.009 lbs.) in 1960 at rates of 1000 per acre (Pond 3) and 5000 per acre (Ponds 2 and 5). Their growth in early and late summer is presented in Table 12. The stocking-rate of 5000 per acre in Pond 2 was more efficient than the rate of 1000 per acre until midsummer, when fish stocked at the rate of 5000 per acre were almost as large as those stocked at the lower rate; thereafter, growth by fish in Pond 3 was more rapid, resulting in fish much larger than those in the other ponds. Nevertheless, the highest yields were obtained with the higher rate of stocking (Ponds 2 and 5).

Two ponds that were stocked in 1963 with 6500 fingerlings per acre, the highest stocking-rate that we have used, yielded the highest poundages that we have obtained in one growing season (1922 lbs./A, av. wt. = 0.33 lbs.; and 2023 lbs./A, av. wt. = 0.33 lbs.).

These results parallel findings reported by Swingle (1959:68-70) in that an increase of poundage and a decrease in average size usually are associated with increased stocking-rates. But, yields varied considerably in adjacent ponds that were stocked at the same rate in the same year (Table 12). An examination of results reported by Swingle (1959), shows that one pond stocked with 3000 catfish per acre yielded more pounds than were obtained with a stocking-rate of 5000 per acre, and another pond stocked with 3000 catfish per acre yielded fewer pounds than a pond where 1032 catfish per acre were stocked.

The variability in yields on the same stocking-rate is evident in results that we obtained with stocking rates of 2000 to 2250 per acre in different years (Table 13). Our formulated feeds (Table 5) were used in 1961 and 1962. Purina Pondfish Feed was used in

TABLE 12.—GROWTH BY CATFISH STOCKED AT DIFFERENT RATES IN OPEN PONDS IN 1960.

POND	Stocking rate/acre	July 29		November 7–9	
		Average length (inches)	Average weight (pounds)	Average length (inches)	Average weight (pounds)
3	1000	7.8	0.17	11.8	0.54
2	5000	7.3	0.14	9.7	0.24
5	5000	5.5	0.07	7.9	0.15

1964. A feeding rate of 7 per cent was used in 1961, 3-5 per cent in 1962, and 2½ per cent in 1964.

Approximately equal yields of channel catfish were obtained in the three ponds stocked with 2000 channel catfish per acre in 1964 (Table 13). Two of these ponds also contained bass (largemouth) and bluegill. When drained, these two ponds yielded the following poundage of each species: channel catfish, 726 and 755 lbs./A; bass, 40.6 and 43.8; bluegill, 66.9 and 63.1; the total poundages of all species were 833.1 and 861.9 lbs./A. Additionally, several hundred young-of-year bluegill, 0.8-3.0 inches long, occurred in both

TABLE 13.—YIELDS OF CHANNEL CATFISH IN ONE GROWING SEASON, AT SIMILAR STOCKING-RATES (FINGERLINGS).

YEAR	Number stocked per acre	Feed used (% protein)	Average weight (pounds)	Yields (lbs./A)
1961	2250	20	0.25	550
	2250	30	0.26	622
	2250	50	0.28	624
	2250	30	0.31	703
	2250	40	0.33	783
1962	2250	20	0.58	1103
	2250	50	0.66	1245
	2250	40	0.70	1314
	2250	30	0.81	1515
1964	2000†	32	0.38	726
	2000†	32	0.39	755
	2000	32	0.40	789

† 350 Bass and 690 bluegill also present per acre.

ponds but were not enumerated nor weighed. The feed-conversion values by catfish in these two ponds were 1.94 and 2.11 as compared to 2.00 in the pond containing 2000 catfish alone. Another pond that was stocked with 3370 fingerling catfish yielded 1399 lbs./A in 1964; the feed-conversion value was 1.60. As stated above, large differences in production were associated with the number of catfish in the ponds (Tables 12 and 13); but the presence or absence of bass and bluegill scarcely affected the production of catfish.

Although the stocking-rate importantly affects the yield that can be obtained from stocks of fingerling catfish at the end of one growing season, other factors influence yields to an even greater extent than does the stocking-rate (see subsequent discussion of carrying capacity and physical-chemical factors in our ponds). Because of wide variation in the yields obtained with similar stocking-rates, our data are inadequate to demonstrate the most advantageous rate. Some generalizations seem possible, however: if the main objective is to obtain a maximum poundage of small fish, a stocking-rate of 5000 or more fingerlings per acre may be desirable. On the other hand, our results indicate that a stocking-rate of 2250 per acre often gives yields almost as high as do higher stocking-rates; the 2250-rate permitted yields that approached the carrying capacity of our ponds. The results obtained in 1960 (Table 12), as well as data in more recent years, suggest that the most efficient method would be to stock at a high rate (5000-6500 per acre), and reduce the population by partial cropping when the fish are 6 to 8 inches long (approx. 0.15 lbs.), and thereafter as they grow larger.

EFFECT OF CROWDING ON GROWTH

The tendency toward decrease in size of fish associated with increased stocking-rates may be due to the effect of physical crowding, or to some minimal space requirement of channel catfish that must be met in order for normal growth to occur. Studies in which fish are grown in aquaria indicate that limited space is a deterrent to growth; but decrease in growth may be dependent on the amount and quality of water present, rather than the dimensions of the tank. Thus catfish might grow well in confined quarters if large amounts of water circulated through the tank.

In 1962, 5, 20, or 50 fish were stocked in three sections (each 15 inches wide, 5 feet long, 30 inches deep) of an experimental trough having a continuous exchange of water, and 5 and 20 fish were stocked in tanks (6 feet long, 4½ feet wide, 27 inches deep) that

were continuously aerated but lacked exchange of water. All fish were fed a 30 per cent protein-ration at a daily rate of about 5 per cent of fish-weight. The number stocked in each unit and the average weight of the fish on various dates are shown in Table 14.

Growth was better in the units having exchange of water rather than aeration. But, even with continuous exchange of water, the highest stocking-rate (50 per section) resulted in decreased growth by the fish. Thus a continuous influx of fresh water seemingly will not allow maximal growth by unlimited numbers of channel catfish (350,000 per acre in this instance). Growth by fish stocked at the rate of 20 per unit (140,000 per acre) was as good as that made by fish stocked at the rate of five per unit (35,000 per acre). However, this growth was much less than that made by fish of comparable size that were stocked in open ponds.

TABLE 14.—AVERAGE WEIGHT (IN GRAMS) OF CHANNEL CATFISH CONFINED IN EXPERIMENTAL TROUGH AND TANKS, 1962. NUMERALS IN PARENTHESES INDICATE NUMBER OF FISH IN EACH OF THE FIVE UNITS.

DATE	Trough section			Tank number	
	1 (50)	2 (20)	3 (5)	4 (20)	5 (5)
June 11	23.8	28.1	22.9	24.0	22.1
June 25	29.7	31.4	26.3	26.3	24.5
July 9	30.7	37.3	38.2	26.7	29.3
July 23	37.1	41.7	42.5	34.5	30.7
August 6	44.2	51.4	49.5	†	33.3
August 20	46.3	55.0	61.3	.....	‡
September 3	52.4	75.6	74.1	.....	.....

† Fish died August 3-4.
‡ Fish died August 7.

Various numbers of fish were stocked in sections of our subdivided ponds (Ponds 10 and 11; Figure 1) in 1964, to ascertain the effects of different degrees of physical crowding of fish in earthen ponds. Each pond was stocked at a relatively low rate of 1620 catfish per acre. However, different sections of the ponds were stocked with 10, 20, 42, or 90 fish so that the degree of crowding varied within each part of the pond. Water mixes freely throughout these ponds so that the fish in each section occupied

water of similar quality. Presumably, metabolites were exchanged throughout the pond and did not accumulate in sections containing more fish. Therefore the effect of crowding itself was tested, rather than the more complex effects that may arise when different stocking-rates are used in separate, open ponds.

The growth-histories (expressed as average weights) of fish in each section in the summer of 1964 are presented in Figures 10 and 11. The weights of fish when stocked and harvested are given in Table 15. When the two ponds were drained, the sizes of the catfish in each section were highly variable. An analysis of variance detected no significant difference ($P \neq .95$) in growth associated with the various degrees of crowding, although catfish stocked at the two lower rates (10 and 20 per section) grew slightly larger than those stocked at the higher rates (42 and 90 per section). On the other hand, the total yield and total gain in weight were eight times as much in sections stocked with 90 fish as in sections stocked with 10 fish. An analysis of variance indicated that growth in Pond 11 was significantly higher ($P = .99$) than that in Pond 10. Gains were consistently higher and conversion of feed to flesh was consistently better for each stocking-rate in Pond 11 than in Pond 10 (Table 15), but the trends in growth under different degrees of crowding were the same in both ponds (Figures 10 and 11).

Source of variation	Degrees of freedom	Mean square	F
Between Ponds	1	3.629	17.2 **
Among Different Numbers Stocked	3	0.530	2.51 n.s.
Interaction	3	0.0256	0.12 n.s.
Error	55	0.2108	

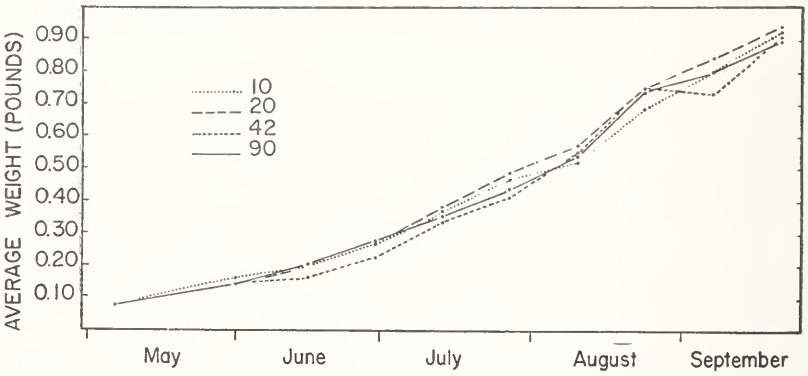

Fig. 10. Patterns of Growth by Channel Catfish in Subdivided Pond 10 in 1964, through 21 September. Within the Pond, Enclosures of Equal Size Contained 10, 20, 42, or 90 Fish. Fish Were Fed (30 Per Cent Protein) at Equivalent Daily Rates (Approximately 3 Per Cent of Weight of Fish in Each Enclosure).

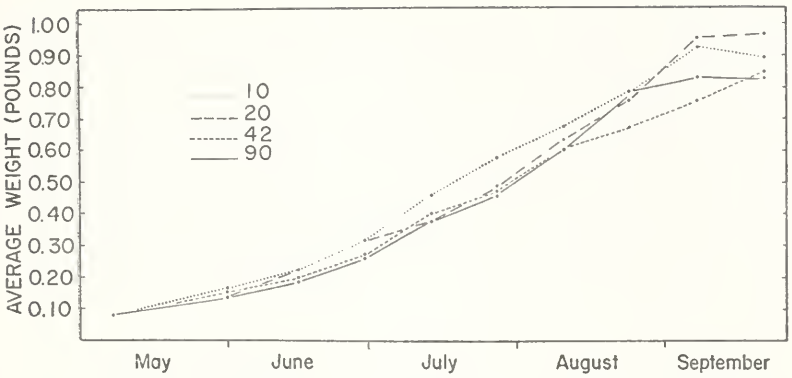

FIG. 11. Patterns of Growth by Channel Catfish in Subdivided Pond 11 in 1964, through 21 September. Within the Pond, Enclosures of Equal Size Contained 10, 20, 42, or 90 Fish. Fish Were Fed (30 Per Cent Protein) at Equivalent Daily Rates (Approximately 3 Per Cent of Weight of Fish in Each Enclosure).

TABLE 15.—GROWTH BY SUBADULT CHANNEL CATFISH IN SUBDIVIDED PONDS IN 1964. TERM OF EXPERIMENT 147 DAYS; PONDS DRAINED 7 OCTOBER.

	Pond number	Number of fish stocked in each section				Totals or average
		10	20	42	90	162
Number of fish recovered	10	10	20	42	90	162
	11	10	20	42	89	161
Total weight of fish stocked	10	0.72	1.48	3.11	6.94	12.25
	11	0.77	1.59	3.21	7.15	12.72
Average weight of fish stocked	10	0.072	0.074	0.074	0.077	0.076
	11	0.077	0.079	0 076	0.079	0.079
Total weight of fish recovered	10	8.75	17.69	33.56	71.69	131.69
	11	10.00	19.31	36.81	80.00	146.12
Average weight of fish recovered	10	0.88	0.88	0.80	0.80	0.81
	11	1.00	0.97	0.88	0.90	0.91
Gain in weight (production)	10	8.03	16.21	30.45	64.75	119.44
	11	9.23	17.72	33.60	72.85	133.40
Pounds of feed used	10	18.97	39.58	76.86	169.66	305 07
	11	17.97	34.26	65.85	141.52	259.60
Conversion feed/gain (lbs.)	10	2.36	2.44	2.52	2.62	2.55
	11	1.95	1.93	1.96	1.94	1.95

Observations of channel catfish in our ponds indicate that they are gregarious. Also, circular depressions visible in the bottom of our ponds when drained, and samples taken with seines, indicate

that catfish aggregate in some parts of the ponds. We found essentially no evidence of agonistic behavior, even under crowded conditions in holding tanks.

The relatively minor effect of physical crowding on the growth of catfish might be expected, considering this gregarious behavior, which may provide new management techniques. Fish might be held in a confined area within a large body of water, simplifying their harvest and, perhaps, enabling more efficient consumption of feed with the advantage of a low stocking-rate in relation to the area of the entire body of water.

CARRYING CAPACITY OF PONDS FOR CHANNEL CATFISH

Little is known about the carrying capacity of waters for different species of fish. European fish-farmers have recognized that there are production-limits of ponds for carp (Bennett, 1962:61). Commercial fish-farmers commonly stock ponds with only enough fish to produce a marketable product at the end of one or two growing seasons. Boccius recognized in 1841 that water as well as land is limited in the quantity it can produce (Bennett, 1962:61).

Swingle and Smith reported in 1938 that ponds stocked with 6500 bluegill-fry yielded approximately 300 lbs./A after one year (Bennett, 1962:61-62). A second year provided no additional growth. In another series of ponds 1300, 3200 and 6500 bluegill-fry yielded fish averaging 4 ounces, 2 ounces and 1 ounce, respectively. The total weight produced was approximately 300 lbs./A in each pond.

One pond stocked with bluegill-fry at the rate of 26,000 per acre (2 lbs. 5 ounces), and another stocked with year-old fingerlings at the rate of 13,000 per acre (180 lbs.) yielded 105 and 92 pounds per acre respectively after one growing season (Swingle and Smith, 1939). Thus the fish in one pond gained approximately 100 pounds per acre, while those in the other lost about 90 lbs./A due to overstocking.

Results like those reported by Swingle and Smith were obtained in our ponds containing channel catfish. The maximum poundage of catfish that our ponds will support naturally is less than 200 lbs./A (Table 1). The variation in total number and weight of fish stocked had little effect upon yields. Total weights of populations apparently fluctuate about a rather uniform level that represents the carrying capacity of that particular environment.

The carrying capacity of a body of water is dependent mainly on its surface area rather than its depth or volume, and is probably

related to the amount of food produced by the body of water (Bennett, 1962:61). The area and depth of the zone of light penetration, where the bulk of the food-supply is produced for fishes, is most important. Carlander (1955:550) found no significant correlation between standing crop (per acre) and area of several lakes and reservoirs. In contrast, the productivity of a body of water apparently is inversely correlated with its depth. Carlander reported a significant ($P = .95$) negative regression of standing crops of fish on the maximum depths of several warm-water lakes.

Theoretically, a pond containing fishes of many kinds and sizes affords the most efficient utilization of available food. Carlander (1955:553-558) reported an increase in standing crop with increase in the number of species present. The total poundage of a given species may be affected by the presence or absence of other species of fish. But in our experiments in which channel catfish were stocked along with bass and bluegill, and did not receive supplemental feeds, the carrying capacity of the ponds for channel catfish was not affected. Growth in these ponds was comparable to that made by catfish stocked alone in other ponds; yields were 110 to 170 pounds of catfish per acre without supplemental feeding (Table 1). Similarly, the presence of bass and bluegill in ponds where catfish were fed did not alter the yields of catfish appreciably (Table 13).

Many factors other than the number of fish present affect the carrying capacity of a pond: age of the pond and changes associated with its aging; changes in conditions of the watershed; seasonal changes; and artificial effects of man—all of which alter the fertility of a pond.

The addition of supplemental feed to a pond containing channel catfish artificially increases the poundage of fish that a pond can support by introducing into the system nutrients that are produced from an outside source. Supplemental feeding allows for standing crops several times greater than those produced without feeding (Tables 12 and 13). Obviously when high poundages are present in a pond the fish must be dependent primarily on the feed added to the pond.

In our early experiments, approximately 1200 lbs./A was the maximum yield that we could obtain with supplemental feeding. Swingle (1957:161) reported yields up to 1242 lbs. of channel catfish per acre in some Alabama ponds, and in later experiments (Swingle, 1959:69) he reported productions as high as 2347 pounds

per acre. Persons who raise channel catfish commercially in Kansas have told us that annual productions in their ponds sometimes exceed 3000 pounds per acre.

The carrying capacity apparently was reached in two of our ponds containing subadult catfish in 1961. All of the channel catfish in both ponds had been held overwinter in Pond 1. On June 13, 1961, half of the fish were transferred to Pond 8 resulting in a stocking rate of 2160 per acre in each pond. Both ponds received a 40 per cent protein feed at a rate of 4-6 per cent of body weight. (The rate was adjusted to 6 per cent at two-week intervals, and was never less than 4 per cent at the end of any two-week period.)

On July 24, 1961, the average lengths and weights of catfish in Ponds 1 and 8 were 11.5 inches and 0.50 pounds, and 11.8 inches and 0.57 pounds, respectively; therefore growth from June 13 to July 24 was almost alike in both ponds. The same amounts of feed were used in both ponds until July 24. Growth proceeded rapidly in early summer, from standing crops of about 500 pounds per acre to 1100 or 1200 pounds per acre. However, from July 10 to August 8, growth apparently ceased despite continued feeding and relatively high oxygen-content (mean oxygen-values in afternoon were above 7.2 ppm in Pond 1, and 6.5 ppm in Pond 8 in this period). The average temperature between July 10 and August 8 was 84° F.

In an attempt to induce further growth by the fish two methods were employed: (1) reduction of the number of fish in Pond 8, and (2) installation of a mechanical aerator in Pond 1 without removing any fish.

On August 8, half the fish were removed from Pond 8, decreasing the stocking-rate to 1080 per acre. The remaining fish resumed growth, and by October 4 almost as many pounds per acre (1100) existed in the pond as were present before thinning. This pond was drained on November 1 and yielded 906 pounds per acre. Thus cropping of the fish in July resulted in a large increase in the total harvest obtained from the pond.

In Pond 1 a mechanical aerator (of a type manufactured by Hinde Engineering Co., Highland Park, Illinois) was installed on August 1. From August 8 to November 1 the aerator was operated approximately 12 hours each night. The growth-rate of the fish increased sharply until October 4, when an estimated 2300 pounds per acre existed in the pond—almost twice the previous "carrying capacity" of 1200 pounds per acre. Pond 1 was drained November 1, 1961, and yielded 2215 pounds per acre.

The high production enabled by aeration of Pond 1 seemingly

rules out any "space factor" as a cause for the limited production of 1200 pounds per acre obtained previously in these ponds. Removal of half the fish in Pond 8 and aeration of Pond 1 may have had a similar effect in reducing the concentration of volatile wastes that (earlier) limited production to about 1200 pounds per acre.

Subsequent experiments utilizing aerators fail to substantiate this hypothesis. Two ponds (2 and 4) were stocked with 840 two-year-old channel catfish per acre, and two ponds (3 and 5) were stocked with 6500 fingerlings per acre in 1963 (Table 16). Ponds 2 and 3 were aerated continuously from June 4 until the date of draining in fall by means of aerators similar to that used in 1961. Some fish were removed in summer for internal examination, mainly for fattiness of livers; thus, the stocking-rates declined gradually (Table 16). The fish in all ponds were fed a ration containing 30 per cent protein, at a daily rate of 2.5 per cent of fish-weight.

Aeration may have been beneficial in ponds containing two-year-old catfish. When drained on September 27, the aerated pond (Pond 2) yielded 267 lbs./A more than the pond that was not aerated (Pond 4). The fish in Pond 2 averaged 0.47 pound heavier, and usually had a slightly higher condition index, than fish in Pond 4.

Aeration seemingly had little effect on growth by fingerling catfish in 1963. Fish in the aerated and non-aerated ponds had the same average weight (0.33 pound) when those ponds were drained on October 3 and 4; however, Pond 5 (not aerated) yielded 97 lbs./A more than Pond 3 because of lesser mortality.

In the ponds that were stocked with fingerlings, the standing crops increased steadily throughout summer, and were higher at the time of draining than were standing crops in ponds containing two-year-old catfish. No increase in standing crops of the latter ponds was evident after mid-July; thereafter, gains made by individual catfish approximately equaled the weight of fish that were removed periodically. Because of the large size of the two-year-old fish, the summer-harvest of them greatly exceeded, in weight, the harvest from ponds stocked with fingerlings. The total yield (poundage of fish removed in summer plus that recovered when ponds were drained) was of the same general magnitude in all four ponds. All four had standing crops, on one or more dates, that exceeded the 1200-pound-level which seemed to be the approximate "carrying capacity" of our ponds in previous experiments.

Artificial aeration did not account in any major way for the high productivity of our ponds in 1963. Chemical data obtained from

TABLE 16.—WEIGHTS (IN POUNDS AND POUNDS/ACRE) AND CONDITION INDEX ("C") OF FINGERLING AND TWO-YEAR-OLD CHANNEL CATFISH IN AERATED (PONDS 2 AND 3) AND NON-AERATED (PONDS 4 AND 5) PONDS IN 1963.

DATE	Stocking rate		Pond 2			Pond 4			Pond 3			Pond 5		
	Ponds 2 & 4	Ponds 3 & 5	Av. wt.	Total wt.	Av. "C"	Av. wt.	Total wt.	Av. "C"	Av. wt.	Total wt.	Av. "C"	Av. wt.	Total wt.	Av. "C"
April 11	.....	6500	.....	.....	.....	.....	.....	.....	0.13	90	.....	0.13	90	.....
June 3	840	6500	1.06	891	33.1	1.02	856	33.1	.04	242	38.2	.05	299	34.7
June 17	840	6500	1.52	1281	38.4	1.36	1144	38.8	.05	343	36.7	.07	437	36.1
July 1	800	6450	1.35	1080	36.8	1.69	1352	43.5	.07	439	32.9	.10	673	34.6
July 15	760	6400	2.10	1596	40.6	1.70	1296	39.6	.12	737	34.6	.14	886	35.3
July 29	720	6350	2.08	1494	40.8	1.88	1351	39.4	.14	902	33.7	.18	1143	33.8
August 12	680	6300	2.15	1458	39.2	2.09	1423	41.1	.23	1435	39.8	.18	1158	33.2
August 26	640	6250	2.50	1600	42.0	2.44	1562	39.9	.27	1718	35.6	.25	1559	31.1
September 9	600	6200	2.65	1590	41.8	2.49	1494	39.3	.29	1786	34.2	.29	1798	32.4
September 27	560	.....	2.73	1531	41.6	2.26	1264	36.6	.....	.....	.....	.....	.....	.....
October 3–4	5720–5940†		.....	.....	.....	.....	.....	.....	.33	1871	34.0	.33	1968	36.1
Summer harvest‡	280	350		574			546			58			61	
Total yield				2105			1810			1929			2029	
Production				1213			954			1843			1941	

† Mortality of 7 and 3.4 per cent in Ponds 3 and 5, respectively. (No mortality in Ponds 2 and 4.)

‡ 50 fish per acre removed from Ponds 3 and 5, and 40 fish per acre removed from Ponds 2 and 4 at bi-weekly intervals June 17-September 9.

these ponds indicate that aeration was not needed, and that the aerators *used* had scant effect on water-quality. (For example, the amount of dissolved oxygen in afternoon remained high in all ponds throughout the summer of 1963, and diurnal variations in dissolved-oxygen were great in aerated as well as in non-aerated ponds; see Figure 13.) Aeration did prevent stratification in Ponds 2 and 3; stratification occurred daily in Ponds 4 and 5 but was interrupted by nocturnal mixing.

Aeration is beneficial only when some factors, presumably chemical, limit the poundage of fish that a pond will support. When dissolved oxygen remains low, or growth of fish is retarded by substances that may be oxidized, aeration can increase the carrying capacity of a pond. Nocturnal aeration, such as employed in 1961, seems most important.

Once the carrying capacity of a pond has been reached, continued feeding (without cropping or aeration) is inefficient, wasteful, and potentially harmful by pollution of the water. This principle applies generally, although the carrying capacity varies from time to time as well as from pond to pond.

Reduction of fish-growth as the carrying capacity is reached is not due to limited "growth-ability" of channel catfish during one growing season. Conditions existing within a pond collectively limit the poundage of catfish that the pond will support. Manipulation of these conditions (as by cropping or aeration) may result in raising, or maintaining at a high level, the carrying capacity of a pond.

PHYSICAL-CHEMICAL CONDITIONS IN EXPERIMENTAL PONDS

The variability of productions of channel catfish in different ponds indicates that the nature of the ponds themselves influences production. Although our ponds are structurally alike and have a common water-source, the physical-chemical properties of the ponds vary temporally as well as from pond to pond. From 1961 through 1964, records were obtained of temperature, dissolved oxygen, alkalinity, pH and dissolved solids by the methods described below.

Methods

Thermistors (Whitney, or Jarrel-Ash Model 26-601) were used to measure temperatures at different depths in the ponds. Measurements usually were taken three times each week near the surface, mid-depth (0.7 m.), and bottom of the ponds (approximately

1.4 m.). Early-morning and mid-afternoon readings were taken in 1962 and 1963, to approximate the maximum and minimum temperatures of the ponds. In 1963, readings were taken once each week at three-hour intervals for a 24-hour period. A recording thermometer operated continuously in one of the ponds.

The dissolved oxygen-content of the ponds was determined by titration using the Winkler Method (Faber, 1955:250-255) in 1961. Subsequently the amount of dissolved oxygen was measured directly in the ponds by means of an oxygen analyzer (Jarrel-Ash Model 26-601). Readings were taken in per cent of saturation, and converted to ppm (Stand. Meth., Faber, 1955:254). Corrections were made for altitude. Values obtained by concurrent use of both methods (analyzer and titration) corresponded closely. All readings above 120 per cent of saturation were evaluated by titration. Oxygen-determinations were made at approximately the same intervals and depths as were the temperature-measurements discussed above, except in 1961 when oxygen-readings were taken only near the surface.

A Beckman Model N meter was used for pH-determinations; readings were taken of the surface-water at intervals discussed under temperature.

Phenolphthalein alkalinity and methyl-orange alkalinity (Stand. Meth., Faber, 1955:35-38) were ascertained by titration of water-samples taken approximately one foot beneath the surface of the ponds. Titrations were performed in the early morning in 1962, 1963, and 1964; in 1963, titrations were made also in mid-afternoon, as well as at three-hour intervals over a 24-hour period, one day a week.

Measurements of the total dissolved solids in the ponds were taken weekly by means of a portable conductivity bridge (Industrial Instruments, Model RC 7P). Specific conductance indicates the total concentration of the ionized constituents of waters. It is clearly related to the sum of the anions, or cations, determined chemically and usually correlates closely with the dissolved residue (Faber, 1955:89-92). The electrical conductivity was corrected to 25° C. and multiplied by a constant (0.65) to obtain the dissolved solids in parts per million (Rainwater and Thatcher, 1960:270).

Temperature

The average afternoon temperatures at the surface of our ponds in 1961, 1962, and 1963 are presented in Figure 12A. Temperatures remained above 25° C. (77° F.) during the greater part of our

experiments (June to mid-September). Subsequently, temperatures dropped considerably (to approximately 15° C. by late October 1961). The least variation in temperature among the three years was in August; temperatures in early and late summer varied considerably in the different years.

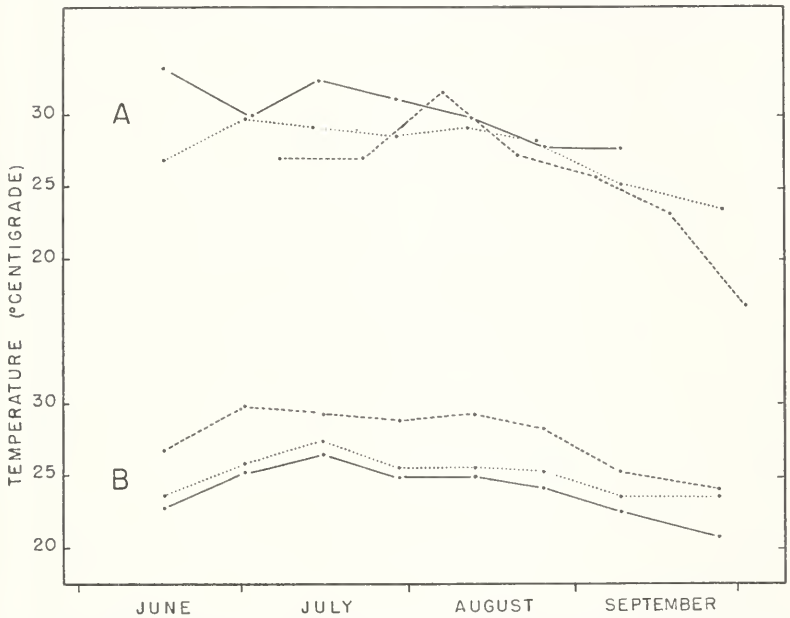

FIG. 12. (A) Surface-temperatures in Experimental Ponds in 1961 (Dash-line), 1962 (Dotted Line), and 1963 (Solid Line). Lines Join Average Values Within Biweekly Intervals in which Data on Growth by Catfish Were Obtained. (B) Surface-temperatures (Dash-line) and Bottom-temperatures (Dotted Line) in Midafternoon, and Temperatures at both Surface and Bottom (Solid Line) in Early Morning, in Experimental Ponds in 1962. Ponds Stratified Daily, but Mixing Overnight Restored Thermal Uniformity. Lines Join Average Temperatures Within Biweekly Periods in which Data on Growth by Catfish Were Obtained.

The surface-temperatures of our ponds in afternoon remained relatively stable during most of our experiments (between 25° C. and 30° C. in 1962); however, temperatures varied several degrees diurnally. The average surface- and bottom-temperatures of all ponds in early morning and mid-afternoon in 1962 are presented in Figure 12B. Although our ponds are relatively small and shallow, their water usually stratified each afternoon and mixed each night. Morning-temperatures were essentially the same from the surface to the bottom of the ponds. Water near the bottom retained approximately the same temperature throughout the day, but the tempera-

ture of the water near the surface increased, resulting in stratification and a definite thermocline in the shallow zone. The degree of stratification decreased in late summer and essentially no stratification occurred at the end of September in 1962. Although fish in our ponds could have remained in water having nearly the same temperature throughout any 24-hour cycle, we doubt that they did so, because of daily oxygen-depletion in the deepest, coolest zone.

When fish are acclimated at various temperatures, metabolic rates do not increase as much as twofold with each 10° C. increase in temperature, and increases in metabolism diminish as the upper lethal temperature is reached (Moss and Scott, 1961:390). Moss and Scott reported that resting channel catfish showed no appreciable increase in their metabolic rate as water-temperatures increased from 25° C. to 35° C. The metabolic mechanisms of channel catfish appear to be highly adaptive. If given sufficient opportunity for temperature-acclimation they tend to operate at the same rate regardless of temperature, at least within the range of 25-35° C. (Moss and Scott, 1961:390). Assuming that these experimental results are applicable to our ponds, the fluctuations in temperature during the summer may have had little effect on periodic growth by channel catfish in these ponds.

In our ponds, growth by catfish in 1961 and 1962 (Figure 3) decreased in late-September of each year, when surface-temperatures were below 25° C. Swingle (1959:66) reported that channel catfish responded best to feeding when surface-waters were warmer than 70° F. (21° C.), and recommended that supplemental feeding be stopped while water temperatures were below 60° F. (15.5° C.). Feeding when water temperatures were below 20° C. in our ponds was inefficient; feeding at such temperatures should only be at a rate sufficient to maintain the fish in satisfactory condition.

Dissolved Oxygen

Dissolved oxygen-levels at the surface of our ponds remained relatively high throughout summer, the average for two-week-intervals being generally higher than six ppm (see Figure 13 for oxygen-levels in four ponds in 1963). Tiemeier and Moorman (1957:169-170) and Tiemeier and Elder (1957:381-383) reported similar oxygen-levels in several farm ponds in Kansas. Weather-conditions (whether day was clear, rainy, windy, calm) and density of plankton-blooms in the ponds influenced the daily variation in the oxygen-levels of our ponds.

The dissolved oxygen of the surface-waters varied a great deal diurnally. The lowest levels, in early morning (approximately 6:30 a. m.), usually were 4-6 ppm in June and July of 1963; subsequently, morning oxygen-levels were usually less than 4 ppm (Figure 13).

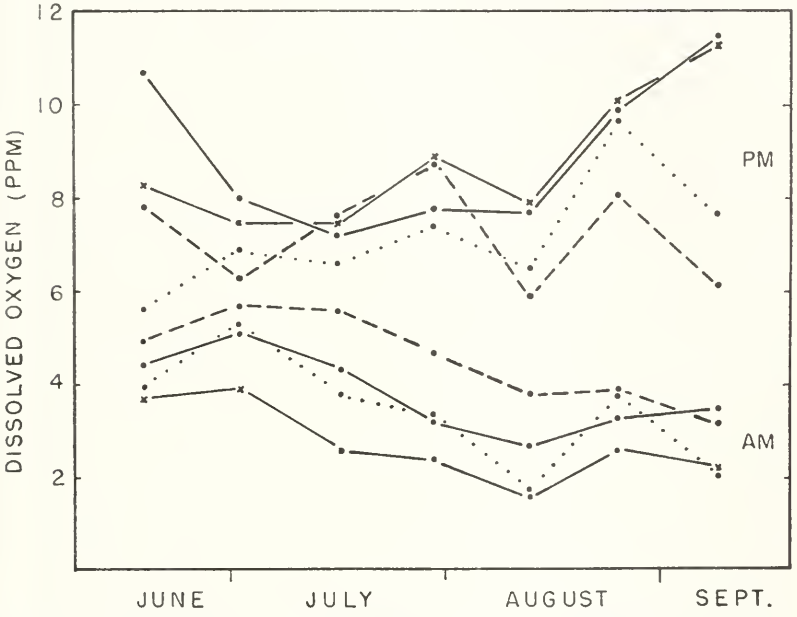

FIG. 13. Dissolved Oxygen in Early Morning (a. m.) and Midafternoon (p. m.) in Four Experimental Ponds in 1963. Lines Join Average Values Within Bi-weekly Periods in which Data on Growth by Catfish Were Obtained. Solid Line Joining Dots Represents Pond 2 (Aerated, Large Fish); Solid Line Joining x-marks, Pond 4 (Not Aerated, Large Fish); Dash-line, Pond 3 (Aerated, Small Fish); Dotted Line, Pond 5 (Not Aerated, Small Fish).

Stratification and mixing occurred daily. Oxygen-concentrations frequently were less than 2 ppm in the deepest part of the ponds during the afternoon. Respiration in the ponds, as well as mixing at night of the oxygen-depleted waters from the bottom with oxygenated surface-waters, contributed to the low oxygen-levels present in the ponds in early morning.

Resting fish of most species consume oxygen at rather constant rates over a wide range of ambient oxygen-tensions (Moss and Scott, 1961:392). Moss and Scott (1961:385-393) found no change in the oxygen-consumption of resting channel catfish that were exposed to oxygen-levels varying from approximately 8 ppm to less than 1 ppm over a 15-day period. Critical dissolved oxygen-levels

were usually slightly less than 1 ppm but increased slightly with rising temperature.

At low levels of dissolved oxygen, oxygen-consumption by fish becomes dependent upon the concentration of oxygen in the environment. The oxygen-level at which this shift to oxygen-dependent metabolism occurs (the incipient lethal level) depends upon the degree of activity of the fish, which influences their oxygen-requirement. Fish entering this phase of metabolism will eventually die unless their activity is reduced or the oxygen-level is increased.

The amount of oxygen necessary to sustain the normal activity that is associated with rapid growth is not known, but seems low in channel catfish. Perhaps the extent of daily fluctuation in dissolved oxygen, as well as the minimal daily oxygen-level, importantly influences the rate of growth. In two ponds in 1962, morning oxygen-levels were less than 2 ppm in the first half of August, but fish in those ponds grew satisfactorily (Figure 3). In 1963, morning oxygen-levels in Pond 4 averaged less than 2 ppm in mid-August, while the average was 4 ppm in Pond 3 (Figure 14). Growth was rapid in both ponds at this time, and was better than the growth-rate in Ponds 2 and 5, which had oxygen-levels intermediate to those in Ponds 3 and 4 during this period (Table 15). But, morning oxygen-levels in Pond 4 remained low for an extended interval, and seemingly affected growth adversely. Morning-readings in this pond were less than 3 ppm through most of the growing season. When Pond 4 was drained, its fish weighed approximately 0.5 pound less than those in a comparable pond (Pond 2) in which oxygen-levels remained above 3 ppm.

We think that low levels of dissolved oxygen inhibited production in an experimental pond where feed containing 50 per cent protein was used in 1961. The *maximal* dissolved-oxygen-level remained below 4 ppm in the pond through most of August and September. Although the minimal daily levels of dissolved oxygen in this pond were not known, subsequent morning and afternoon determinations suggest that the oxygen-levels at night were critically low. The fish probably entered an oxygen-dependent phase of metabolism, and their activity decreased correspondingly. During this period the catfish apparently stopped eating, because feed accumulated in the pond; and, decomposition of the unused feed undoubtedly contributed to the oxygen-deficit. Fish in this pond gave no evidence of stress by surfacing, but their growth essentially stopped.

Observations of similar effects of low oxygen-levels on other species have been reported. For example, Shepard (1955:428) reported that speckled trout held at oxygen-levels slightly above the incipient lethal level were sluggish, fed poorly and were susceptible to disease.

The effects of mechanical aeration of ponds, on the production of channel catfish, were discussed under the heading "Carrying Capacity of Ponds."

pH-Values

Average pH-values of seven experimental ponds in 1963 are presented in Table 17. In early morning, pH-readings were usually slightly below 8, and pH-levels in afternoon were usually less than 9. Swingle (1961:72) reported that waters ranging in pH from 6.5 to 9.0 before daybreak are generally the most desirable for pondfish production; waters in this range are capable of giving highest productions if the level of fertility is adequate. No seasonal trend in pH-values was evident in our ponds. The most obvious changes in the pH of our ponds occurred diurnally. Afternoon-values were consistently higher than morning-readings (Table 17), due to utilization of free CO_2 and HCO_3 in photosynthesis in daytime. Thus the measure of the diurnal fluctuation of pH gives some indication of the basic productivity of a pond, although buffering action within ponds influences fluctuations in pH. Ponds that received supplemental feeds (and consequently had high standing crops of fish) tended to show larger diurnal fluctuations in pH than ponds in which fish were not fed. The feed may have had both direct and indirect fertilizing effects that resulted in an increase in natural productivity in the ponds, reflected by increased diurnal fluctuations in pH. In ponds having comparable stocks of fish, aeration reduced the diurnal fluctuation of pH.

Alkalinity

Total alkalinity expresses concentrations of calcium and carbon dioxide, two substances directly necessary to plant-life; on the other hand, the alkalinity is itself affected by the entire biological and chemical systems of waters. Therefore total alkalinity has been used as a rough index of the productivity of waters (Moyle, 1956: 310).

Water having a low total alkalinity usually has low concentrations of other salts including phosphorus compounds. Such water usually is infertile and lacks dense plankton-populations, according to Moyle.

TABLE 17.—AVERAGE pH IN EARLY MORNING (a. m.) AND AMOUNT OF CHANGE IN pH BY MID-AFTERNOON (Δ) IN SEVEN PONDS IN 1963.

POND	Number of fish	June 3–17		June 18–July 1		July 2–15		July 16–29		July 30–August 12		August 13–26		August 27–September 9	
		a. m.	Δ	a. m.	Δ	a. m.	Δ	a. m.	Δ	a. m.	Δ	a. m.	Δ	a. m.	Δ
No Supplemental Feed Used															
6	75 fingerlings....	8.2	0.5	8.3	0.1	8.1	0.2	8.2	0.3	7.8	0.6	8.7	0.3	8.7	0.3
1	225 fingerlings....	8.2	0.2	8.1	0.3	8.0	0.3	7.9	0.5	7.7	0.6	8.0	0.5	8.1	0.7
9	225 fingerlings....	8.3	0.2	8.3	0.2	8.3	0.3	8.2	0.6	8.6	0.4	8.4	0.3	.....	.....
Received Supplemental Feed															
3	650 fingerlings....	7.9	0.4	7.9	0.2	8.1	0.3	8.5	0.6	7.4	0.4	7.5	0.8	7.3	0.4
5	650 fingerlings....	8.0	0.6	7.9	0.4	7.7	0.5	7.4	1.0	7.3	0.9	7.6	0.9	7.4	1.1
2	84 subadults.....	7.6	1.0	8.0	0.6	7.7	0.8	7.5	0.9	7.5	0.8	7.7	1.0	7.7	1.0
4	84 subadults.....	7.6	0.9	7.7	0.7	7.7	0.6	7.6	1.0	7.3	1.0	7.5	1.4	7.4	1.7

TABLE 18.—AVERAGE TOTAL ALKALINITY (IN PPM) IN EARLY MORNING (A. M.) AND AMOUNT OF CHANGE BY MID-AFTERNOON (Δ) IN SEVEN PONDS IN 1963.

POND	Number of fish	June 3–17		June 18–July 1		July 2–15		July 16–29		July 30–August 12		August 13–26		August 27–September 9	
		a. m.	Δ	a. m.	Δ	a. m.	Δ	a. m.	Δ	a. m.	Δ	a. m.	Δ	a. m.	Δ
No Supplemental Feed Used															
6	75 fingerlings....	132	−7	123	−5	100	−2	83	−2	86	−2	86	−1	76	0
1	225 fingerlings....	121	−6	117	0	131	−9	83	4	90	−6	81	−7	65	4
9	225 fingerlings....	.....	.....	114	−1	109	−2	68	−8	57	−2	52	−1	68	−3
Received Supplemental Feed															
3	650 fingerlings....	121	0	119	1	118	−4	75	−10	92	−1	92	−3	90	1
5	650 fingerlings....	127	−3	113	3	101	−1	96	−1	101	−5	87	−3	85	1
2	84 subadults.....	103	−10	123	2	115	−5	119	−5	148	−6	135	−2	125	−6
4	84 subadults.....	99	1	134	−7	140	2	117	−2	130	0	102	0	105	2

He reported (1949:324) that ponds where total alkalinity was less than 40 ppm did not yield as many pounds of fish as ponds with harder waters. He considered a total alkalinity of 40 ppm to be a useful natural separation-point between soft and hard waters. Carlander (1955:551-552) found a significant increase in standing crops per acre with increased alkalinity (up to 200 ppm) in trout-lakes, in warm-water lakes and in reservoirs.

Phenolphthalein alkalinity was usually absent in our ponds, and when present occurred only in mid-afternoon, associated with high pH-values. Thus, bicarbonates essentially comprised the total alkalinity in our ponds. The average alkalinities for two-week periods in early morning, and the change by mid-afternoon, are presented in Table 18. Total alkalinity usually remained within the range of 65-150 ppm, and seemingly was at levels conducive to good growth by fish. In most ponds the total alkalinity decreased in the course of the summer. This decrease was especially prominent in ponds that did not receive supplemental feeds.

Diurnal variation in alkalinity usually was less than 10 ppm; morning-readings usually were slightly higher than those in mid-afternoon.

Total Dissolved Solids

The total dissolved solids remained within the range of 200-500 ppm in all of our ponds (see Table 19 for levels that occurred in 1963). In most instances, all ponds had similar levels of dissolved solids at a given time. The range of dissolved solids increased from 200-300 ppm during June and July to levels of 300-450 ppm in August and September. The highest levels occurred in early September, the last period in which measurements were taken. It is noteworthy that the seasonal trend in total dissolved solids was opposite to that in alkalinity—the former increasing as the latter decreased.

CORRELATION OF PHYSICAL-CHEMICAL CONDITIONS WITH PRODUCTION

At the start of each set of experiments in our ponds, many factors that influence production are subject to our control. The size and location of the ponds are similar, and the following factors can be constant: source of water and date of filling of ponds, kind, number, size, and date of stocking of fish; kind of feed and daily feeding-rate. In practice one (or more) of the factors listed has been

Table 19.—Total Dissolved Solids (in ppm) in Seven Ponds in 1963. Averages of Several Readings in Mid-afternoon Within Each Interval.

Pond	June 3–17	June 18–July 1	July 2–15	July 16–29	July 30–August 12	August 13–26	August 27–September 9
No Supplemental Feed Used							
6	228	214	224	247	319	346	426
1	266	250	268	280	334	392	428
9	220	198	230	216	316	339	442
Received Supplemental Feed							
3	241	228	218	247	304	336	430
5	242	224	240	272	322	374	430
2	344	304	270	274	339	366	386
4	226	319	290	302	336	356	372

varied from pond to pond, for purposes of testing the effect of that factor on fish-production.

As experiments progress in earthen ponds like ours, additional variables arise. Some of these new variables may be correlated with the principal variable being tested. For example, if feeds having different protein levels are being tested, and one of the feeds is superior to others, differences in weight-gain by the fish, their average weight, and the standing crop follow automatically. These differences may induce others, especially in chemical qualities of the water, and the latter differences may in turn affect subsequent growth by the catfish.

An understanding of the interrelationships of these changes would have value in pond-management. If the physical-chemical conditions that are most favorable for growth of fish can be identified, attempts to establish and maintain those conditions are possible. Even if such attempts fail, knowledge of the relationship of fish-growth to water-quality would enable appropriate adjustments (of feeding-rates, for example) in response to uncontrolled changes in water-quality.

Correlation-coefficients (r) were calculated for variable factors in seven of our ponds in 1963. In that year, we obtained data on growth of fingerling catfish that were not fed (were reliant on food that occurred naturally in the ponds), and on fingerling and subadult catfish that were fed equivalent daily amounts of pelleted rations (Tables 16 and 20).

In Table 21, correlation-coefficients are presented for several variables in ponds in which fish were not fed (Ponds 1, 6, and 9); and, separately, the corresponding correlation-coefficients are given for data from all ponds in which supplemental feed was used (Ponds 2, 3, 4, and 5). The data pertaining to fed fish are subdivided in Table 22, to permit separate analysis of the results in ponds that contained large numbers of small fish (Ponds 3 and 5), and in ponds stocked with small numbers of larger fish (Ponds 2 and 4).

Each variable factor compared is listed in the left-hand column of each of the two tables (21 and 22), together with a numeral that identifies that same factor at the top of each table. "Average weight" is equivalent in effect to the current standing crop where equal numbers of fish were present, as in Ponds 2 and 4, and Ponds 3 and 5 (Table 22). "Condition index" reflects variations in the "plumpness" of fish on the different dates when ponds were sampled. "Δ weight" represents the gain (or loss) from one sampling-date to the next (a 2-week interval). "Former standing crop"

TABLE 20.—GROWTH BY FINGERLING CHANNEL CATFISH THAT RECEIVED NO SUPPLEMENTAL FEED IN 1963. (PONDS 1 AND 9 CONTAINED 2250 CATFISH PER ACRE; POND 6 CONTAINED 600 TO 750 CATFISH PER ACRE.)

DATE	Pond 1		Pond 9		Pond 6	
	Average weight	Total weight	Average weight	Total weight	Average weight	Total weight
April 2	0.013	3.02	0.013	3.02	0 013	1.01
June 3	.050	11.34	.038	8.64	.064	4.80
June 17	.064	14.40	.046	10.44	.100	7.50
July 1	.073	16.38	.050	10.89	.103	7.21
July 15	.066	14.94	.057	11.88	.109	7.35
July 29	.068	15.39	.054	12.15	.078	5.07
August 12	.086	19.35	.058	13.05	.097	6.44
August 26	.075	16.92	.....	.....	.129	8.40
September 9	.074	16.56	.059	13.20	.133	7.98
October 16–17	.074	16.25	.052	10.87	.154	8.93

represents the total poundage of fish on the last previous date of sampling. The "a. m." and "p. m." values of temperature and other factors approximate the minimal and maximal daily values, and are averages of values recorded on several days within the intervals between sampling-dates for catfish. "Δ temperature" (or Δ oxygen, Δ pH, Δ alkalinity) represents the average *difference* between morning- and afternoon-values for that factor.

The correlation-coefficients were calculated from absolute values of the data. Correlation-coefficients were calculated using logarithmic transformations also ($\log y = x$, $y = \log x$, and $\log y = \log x$), but such transformations yielded no information additional to that obtainable without transformation.

Correlations with Average Weight

In ponds where fish were not fed, diurnal change in the amount of dissolved oxygen was the only variable tested that was significantly correlated with the average weight of the fish ($r = .44$); these same two factors were correlated ($r = .62$ to $.68$) in ponds where fish were fed. In the latter ponds, average weights were negatively correlated (−.48 to −.66) with morning-oxygen, but posi-

TABLE 21.—CORRELATION COEFFICIENTS ($\times 100$) OF VARIABLES TESTED IN 1963 IN PONDS WHERE FISH WERE NOT FED (UPPER HALF OF MATRIX, PONDS 1, 6, AND 9), AND IN PONDS WHERE FISH WERE FED (LOWER HALF OF MATRIX, PONDS 2, 3, 4, AND 5). SIGNIFICANT VALUES ITALICIZED: IN UPPER HALF OF MATRIX, DEGREES OF FREEDOM = 19, VALUES $\geq$ 43 *, VALUES $\geq$ 55 **; IN LOWER HALF OF MATRIX, DEGREES OF FREEDOM = 27, VALUES $\geq$ 37 *, VALUES $\geq$ 47 **. Δ SIGNIFIES "DIURNAL CHANGE IN." FURTHER EXPLANATION IN TEXT.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Average weight	1		20	*45*	*–55*	–34	–08	–11	29	09	13	21	23	19	23	*44*	31	–02
Condition index	2	–25		*51*	*–50*	38	*66*	22	02	*75*	*78*	00	29	*–63*	*60*	–21	*43*	–40
Weight-gain	3	08	*–39*		*–46*	03	22	25	27	23	30	07	16	–07	29	05	*62*	10
Former standing crop	4	*89*	*–52*	07		–30	–35	–25	–20	–23	–27	–34	–16	37	–21	03	–32	33
Temperature	a. m. 5	–36	05	–08	–27		*74*	–16	*–54*	34	36	–33	*–53*	*–72*	11	*–45*	20	–20
	p. m. 6	*–71*	10	06	*–63*	*67*		–20	–33	*62*	*64*	–25	*–49*	*–72*	*75*	–17	30	–28
Oxygen	a. m. 7	*–62*	32	–19	*–67*	–08	15		*57*	–07	–06	*67*	*60*	–07	–14	–37	01	–29
	p. m. 8	*37*	*–56*	16	*39*	–31	–33	–14		–38	–35	*72*	*85*	*49*	05	*55*	08	02
Alkalinity	a. m. 9	–26	*–49*	00	–01	04	07	–05	–06		*99*	–26	*–66*	*–63*	*58*	–36	18	*–50*
	p. m. 10	–26	*–52*	–01	–01	10	09	–04	–02	*98*		24	*–64*	*–63*	*60*	–34	30	*–50*
pH	a. m. 11	*–66*	20	–17	*–62*	07	27	*76*	–03	02	07		*79*	14	–05	13	11	*–52*
	p. m. 12	05	–34	15	07	–22	–02	–01	*72*	–13	–08	36		*54*	–21	37	03	11
Dissolved solids	13	*86*	–24	01	*82*	*–51*	*–69*	*–58*	*43*	–14	–14	*–62*	06		–34	*62*	–15	*53*
Δ Temperature	14	*–59*	19	16	*–57*	–11	*67*	27	–13	06	02	29	20	*–41*		20	25	–21
Δ Oxygen	15	*62*	*–60*	23	*66*	–20	–33	*–65*	*84*	–02	01	*–43*	*56*	*65*	–25		09	31
Δ Alkalinity	16	01	–12	–06	00	33	10	09	23	–21	–02	25	25	01	–20	13		–14
Δ pH	17	*58*	*–49*	28	*58*	–27	–24	*–63*	*70*	–14	–13	*–48*	*64*	*56*	–05	*88*	03	

TABLE 22.—CORRELATION COEFFICIENTS ($\times 100$) OF VARIABLES TESTED IN 1963 IN PONDS HAVING MANY FINGERLING CATFISH (UPPER HALF OF MATRIX, PONDS 3 AND 5), AND IN PONDS HAVING FEW LARGE CATFISH (LOWER HALF OF MATRIX, PONDS 2 AND 4). SIGNIFICANT VALUES ITALICIZED; $\geqslant 51$ *, $\geqslant 64$ **; DEGREES OF FREEDOM = 13. Δ SIGNIFIES "DIURNAL CHANGE IN."

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Average weight	1		–43	44	*97*	–40	*–74*	*–66*	24	*–72*	*–79*	*–70*	–19	*91*	*–56*	*68*	–04	*57*
Condition index	2	37		–50	–32	17	48	22	–44	45	45	19	–22	–34	44	–49	–19	–47
Weight-gain	3	–16	30		20	–08	–31	01	29	–33	–37	–14	03	20	–31	20	–08	20
Former standing crop	4	*73*	10	–47		–42	*–73*	*–72*	18	*–69*	*–75*	*–71*	–22	*93*	*–52*	*68*	–02	*55*
Temperature	a. m. 5	–43	–08	–14	–32		*55*	06	–28	–01	08	30	07	*–56*	–16	–25	44	–26
	p. m. 6	*–76*	–17	20	*–74*	*80*		16	–25	50	*58*	42	32	*–67*	*73*	–31	18	–10
Oxygen	a. m. 7	–48	–32	–13	–43	–20	10		11	45	48	*76*	14	*–71*	14	*–67*	–04	*–70*
	p. m. 8	*51*	–08	–11	22	–50	–43	–05		*–51*	–48	25	*67*	17	–07	*66*	39	49
Alkalinity	a. m. 9	12	29	–32	44	02	–31	–31	–45		*98*	17	–28	*–55*	*60*	*–72*	–50	*–52*
	p. m. 10	12	35	–36	40	09	–30	–23	–43	*97*		28	–18	*–63*	*62*	*–72*	–34	*–52*
pH	a. m. 11	–42	–17	–22	–19	–29	–04	*81*	–13	11	13		*–62*	*–72*	26	–39	45	–42
	p. m. 12	48	–19	03	25	*–71*	–50	05	*78*	*–52*	*–59*	–04		–22	33	40	*62*	45
Dissolved solids	13	*67*	09	–22	*51*	*–57*	*–78*	–24	*72*	13	17	–19	49		–34	*66*	–15	*57*
Δ Temperature	14	*–67*	–16	*51*	*–52*	–03	*58*	43	–05	*–55*	*–61*	31	13	*–52*		–16	–14	09
Δ Oxygen	15	*67*	10	–03	*68*	–31	–41	*–57*	*85*	–21	–23	*–53*	*62*	*72*	–26		32	*90*
Δ Alkalinity	16	03	25	14	–02	25	05	31	08	–14	11	06	–25	17	–25	–10		21
Δ pH	17	*63*	–06	15	*55*	–41	–38	–43	*70*	–48	*–54*	*–60*	*82*	50	–07	*80*	–24	

tively correlated (.24 to .51) with afternoon-oxygen. These relationships probably indicate effects of (1) plankton-blooms that commonly develop where standing crops of fish are high, causing high afternoon-oxygen through photosynthesis, and (2) high respiration-demands by catfish and associated organisms, causing oxygen-depletion nocturnally.

Temperatures and daily change in temperature correlated negatively (−.36 to −.76; −.54 to −.67) with size of fish, simply because the catfish were largest in late-season when temperatures were declining and when daily fluctuations in temperature were least.

Alkalinities in morning and afternoon were significantly correlated (negatively, $r = -.71$ and $-.79$) with the average weights of catfish in ponds 3 and 5 but not in other ponds. Correlations of size with diurnal change in alkalinity were not significant in any ponds, and were especially low where fish were fed.

Diurnal change in pH and morning-pH were correlated with the size of catfish receiving supplemental feeds ($r = +.57$ and $+.63$; $-.42$ and $-.70$). The afternoon-pH was less significant, perhaps because upward trends in pH in daytime were inhibited by buffering agents in the ponds. Correlations of pH with average weights were low for fish reliant on natural foods. The pH in early morning was lowest in ponds where fish were fed, due to indirect effects of respiration by the far greater poundages of fish in those ponds than in ponds 1, 6, and 9. Afternoon-pH was approximately the same in all ponds; thus, the diurnal change in pH was less in the latter group of ponds.

Total dissolved solids were highly correlated with the average weights of catfish that were fed ($r = .67$ and $.91$), but not with weights of those subsisting on natural food ($r = .19$). The high poundages of fish in ponds 2, 3, 4, and 5, as well as the increasing amounts of supplemental feed that were used in those ponds, probably contributed to the total dissolved solids, explaining their increase as the average weight (and standing crop) of the fish increased.

Correlations with Condition-index

The condition index of catfish may indicate whether conditions are favorable or unfavorable for growth; catfish living in situations favorable for growth should be more plump (in better condition) than those living under conditions unfavorable for growth.

Afternoon-temperatures and diurnal changes in temperature were significantly correlated ($r = .66$ and $.60$) with condition indices of channel catfish that were not fed. Oxygen-levels in afternoon and

diurnal changes in oxygen content were negatively correlated ($r = -.56$) with the condition index of fish that were fed (Ponds 2, 3, 4, 5). This effect was most pronounced in ponds that contained fingerling catfish. Alkalinity and diurnal changes in alkalinity were highly correlated ($r = .75$ and $.78$; $r = .43$) with the condition index of catfish that were not fed. Fish that were fed reflected positive but nonsignificant correlations of condition index with alkalinity in ponds having fish of comparable size (2 and 4; 3 and 5).

Diurnal changes in pH were significantly correlated (negatively, $-.49$) with condition indices among fed fish, but only when Ponds 2, 3, 4, and 5 were considered together. As in the case of afternoon oxygen-levels, changes in pH were most important in those ponds containing fingerling catfish (3 and 5).

Total dissolved solids were significantly correlated (negatively, $r = -.63$) with condition indices only in ponds where supplemental feeds were not used.

Correlations with Changes in Weight

Periodic changes in the weight of the fish were highly correlated ($r = .62$) with the diurnal change in alkalinity in ponds where fish were not fed. Correlations were low for these variables in the ponds where supplemental feed was used. Absolute values of morning and afternoon alkalinity had low but positive correlation ($r = .30$ and $.23$) with changes in weight among unfed fish. In ponds where fish were fed, these correlations were negative ($r = -.32$ to $-.37$). As mentioned before, alkalinity is often used as an indicator of the productivity of waters. In Ponds 1, 6, and 9, where only natural food was available to the catfish, their growth-rate declined as alkalinity declined. The opposite relationship existed in ponds where catfish were fed; large gains in weight occurred despite declining levels of alkalinity during summer.

Diurnal changes in temperature were correlated ($r = .51$) with changes in weight of the subadult catfish. Among the other groups of fish, correlations with change in temperature were not significant; and, absolute temperatures were not significantly correlated with change in weight of fish in any ponds, within the term (3 months) of our records.

SUMMARY

Production of channel catfish under various experimental conditions was carried on in $\frac{1}{10}$-acre earthen ponds and other facilities of the State Biological Survey at Lawrence, mostly from 1960 through 1964.

1. The weight of channel catfish that our ponds supported without supplemental feeding was 98 to 183 pounds per acre.

2. By daily feeding of pelleted rations, yields of 550 to 2215 pounds of channel catfish per acre were obtained.

3. In tests of synthetic diets, force-feeding of gelatin capsules to channel catfish was more successful than force-feeding by means of syringes; but, neither method enabled rapid gains by fish confined in concrete troughs.

4. *Ad lib* feeding of synthetic diets to catfish in troughs indicated that the carbohydrate constituent as well as the percentage of protein in the diet influences weight-gain by these fish. In diets having low protein-content, growth was better on rations containing starch than on rations containing dextrin, sucrose, or cellulose. Differential effects of the carbohydrate constituent diminished as the protein content increased.

5. In open ponds and subdivided ponds, supplemental feeds containing 30 per cent protein produced as many pounds of catfish as did feeds containing larger amounts of protein. Gains made on feeds containing 20 per cent protein were consistently less than those obtained on feeds containing higher levels of protein.

6. Catfish that received supplemental feeds had a higher condition index than did wild catfish. The difference in condition index of fed *vs.* wild catfish diminished as the fed fish grew larger and their standing crop increased in ponds.

7. Experiments in subdivided ponds and in open ponds indicated that feeding-rates of two to three per cent of fish-weight per day probably are the most favorable rates for economic production of channel catfish.

8. High stocking-rates (5,000 or more fingerlings per acre) usually resulted in higher yields of fish than did lower stocking-rates (2,000-2,500 fingerlings per acre), at some sacrifice in the average size of individual fish.

9. The carrying capacity of our ponds varied from year to year. Catfish ceased to grow, and lost weight, in late summer and early autumn in most ponds—when their standing crops were highest and the water-temperature began to decline. Weight-loss occurred in mid-summer in some ponds having high standing crops of fish.

10. Stresses caused by critically low oxygen-levels (less than 3 ppm) seemingly retarded growth by channel catfish, although they signaled their distress by surfacing only when oxygen-levels were

less than 1 ppm. Fish affected by these conditions grew rapidly after partial cropping, or nocturnal aeration, of the ponds.

11. The pH of our ponds was consistently between 7 and 9. Diurnal changes in pH often exceeded seasonal changes, and exceeded differences in pH between ponds where fish were fed or not fed.

12. The total alkalinity of our ponds varied from approximately 50 ppm to approximately 150 ppm. Diurnal change in alkalinity was slight. The alkalinity of most ponds declined in late summer.

13. Total dissolved solids in our ponds varied from approximately 220 ppm to approximately 450 ppm, and were highest in late summer.

14. Where fish were not fed, their growth-rate and condition index were positively correlated with total alkalinity of the ponds, and with the extent of diurnal change in alkalinity. As the average weight of the fish increased the diurnal fluctuation of dissolved oxygen increased. Generally, the growth-rate and condition index of the catfish declined (1) as the standing crop increased, (2) as the alkalinity decreased, and (3) as the oxygen-level became more variable within each 24-hour cycle. Levels of pH and dissolved oxygen were highly correlated in these ponds.

15. Where fish were fed, their growth-rate was not found to correlate highly with alkalinity nor with other chemical factors that were analyzed. But, the condition index of the fish was lowest when daily values of dissolved oxygen and of pH were most variable. When the average weight (and standing crop) of fish was greatest, daily fluctuations in pH and oxygen-content were extreme, total dissolved solids were highest, and alkalinity was lowest.

16. Where fish were fed, production was poor (feed was not utilized well) when water-temperatures fell below 70° F. in early autumn.

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LITERATURE CITED

Bailey, R. M., and Harrison, H. M., Jr.
1948. Food habits of the southern channel catfish (*Ictalurus lacustris punctatus*) in the Des Moines River, Iowa. Trans. Amer. Fish. Soc., 75:110-138.

Ball, R. C.
1952. Farm pond management in Michigan. Journ. Wildl. Mgt., 16(3): 266-269.

Bennett, G. M.
1962. Management of artificial lakes and ponds. Reinholt Publ. Corp., New York, ix + 283 pp.

Brown, L.
1942. Propagation of the spotted channel catfish (*Ictalurus lacustrus punctatus*). Trans. Kansas Acad. Sci., 45:311-314.

Buck, D. H.
1956. Effects of turbidity on fish and fishing. Rept. Oklahoma Fish. Research Lab., 56:1-62.

Buhler, D. R. and Halver, J. E.
1961. Nutrition of Salmonoid fishes. IX. Carbohydrate requirements of chinook salmon. Journ. Nutrition, 74:307-318.

Canfield, H. L.
1947. Artificial propagation of those channel cats. Prog. Fish-Cult., 9:27-30.

Carlander, K. D.
1950. Handbook of freshwater fishery biology. Wm. C. Brown Co., Dubuque, Iowa. v + 281 pp.
1955. The standing crop of fish in lakes. Journ. Fish. Res. Bd. Canada, 12(4):543-570.

Clemens, H. P., and Sneed, K. E.
1957. The spawning behavior of the channel catfish, *Ictalurus punctatus*. U. S. Fish and Wildlife Service, Special Sci. Rept. Fish. No. 219. ii + 11 pp.

Davis, J.
1959. Management of channel catfish in Kansas. Misc. Publ. Univ. Kansas Mus. Nat. Hist., 21:1-56.

DeLong, D. C., Halver, J. E., and Mertz, E. T.
1958. Nutrition of Salmonoid fishes. VI. Protein requirements of chinook salmon at two water temperatures. Journ. Nutrition, 65: 589-599.

Faber, H. A. (Editor)
1955. Standard methods for the examination of water, sewage and industrial wastes (tenth edition). Amer. Public Health Assoc., Inc., New York, N. Y., xix + 522 pp.

Finnell, J. C., and Jenkins, R. M.
1954. Growth of channel catfish in Oklahoma waters. Rept. Oklahoma Fish. Research Lab., 41:1-37.

Halver, J. E., and Coates, J. E.
1957. A vitamin test diet for long term feeding studies. Prog. Fish-Cult., 19(3):112-118.

Hansen, D. F., Bennett, G. W., Webb, R. J., and Lewis, J. M.
1960. Hook-and-line catch in fertilized and unfertilized ponds. Bull. Illinois Nat. Hist. Surv., 27(5):345-390.

HASTINGS, C. E., and CROSS, F. B.
1962. Farm ponds in Douglas County, Kansas, with reference to their use and management for fish production. Misc. Publ. Univ. Kansas Mus. Nat. Hist., 29:1-23.

HICKLING, C. F.
1962. Fish Culture. Faber and Faber, London. 295 pp.

LENZ, G.
1947. Propagation of catfish. Prog. Fish-Cult., 9:231-233.

MARZOLF, R. C.
1957. The reproduction of channel catfish in Missouri ponds. Journ. Wildl. Mgt., 21:22-28.

MCLAREN, B. A., HERMAN, E. F., and ELVEHJEM, C. A.
1946. Nutrition of rainbow trout; studies with purified rations. Arch. Biochem., 10:433-441.

MORRIS, A. G.
1939. Propagation of channel catfish. Prog. Fish-Cult., 44:23-27.

MOSS, D. D., and SCOTT, D. C.
1961. Dissolved-oxygen requirements of three species of fish. Trans. Amer. Fish. Soc., 90(4):377-393.

MOYLE, J. B.
1949. Some indices of lake productivity. Trans. Amer. Fish. Soc., 76:322-334.

1956. Relationships between the chemistry of Minnesota surface waters and wildlife management. Journ. Wildl. Mgt., 20(3):303-320.

NAIL, M. L.
1965. The protein requirement of channel catfish, *Ictalurus punctatus* (Rafinesque). Proc. Annual Conf. Southeastern Game and Fish Comm. for 1962, pp. 307-316.

PHILLIPS, A. M., *et al.*
1940. Carbohydrate utilization by brook trout. Cortland Hatchery Report, 9:24-25.

1963. The utilization of calorie sources by brook trout and by lake trout. Cortland Hatchery Report, 31 (for 1962):35-49.

RAINWATER, F. H., and THATCHER, L. L.
1960. Methods for collection and analysis of water samples. Geological Survey Water-Supply Paper 1454, 301 pp.

SHELL, E. W.
1963. Effects of changed diets on the growth of channel catfish. Trans. Amer. Fish. Soc., 92(4):432-434.

SHEPARD, M. P.
1955. Resistance and tolerance of young speckled trout (*Salvelinus fontinalis*) to oxygen lack, with special reference to low oxygen acclimation. Journ. Fish. Res. Bd. Canada, 12(3):387-433.

SNOW, J. R.
1962. A comparison of rearing methods for channel catfish fingerlings. Prog. Fish-Cult. 24(3):112-118.

STEEL, R. G. D., and TORRIE, J. H.
1960. Principles and procedures of statistics. McGraw-Hill Book Co., Inc., xvi + 481 pp.

SWINGLE, H. S.
1947. Experiments on pond fertilization. Bull. Ag. Exp. Sta., Alabama Poly. Inst., 264:1-34.

1957. Preliminary results on the commercial production of channel catfish in ponds. Proc. 10th Annual Conf. Southeastern Game and Fish Comm., 1956:160-162.

1959. Experiments on growing fingerling channel catfish to marketable size in ponds. Proc. 12th Annual Conf. Southeastern Game and Fish Comm., 1958:63-72.

1961. Relationship of pH of pond waters to their suitability for fish culture. Proc. Pacific Sci. Congress 9 (1957), Vol. 10, Fisheries, 72-75.

Swingle, H. S., and Smith, E. V.
1939. Increasing fish production in ponds. Trans. North American Wildl. Conf., 4:332-338.

Swingle, W. E.
1964. Length-Weight Relationships I and II, IBM 1620, Fortran/Format. Trans. Amer. Fish. Soc., 93(3):318-319.

Tanner, H. A.
1960. Some consequences of adding fertilizer to five Michigan trout lakes. Trans. Amer. Fish. Soc., 89(2):198-205.

Tiemeier, O. W.
1957. Notes on stunting and recovery of the channel catfish. Trans. Kansas Acad. Sci., 60(3):294-296.

1962. Increasing size of fingerling channel catfish by supplemental feeding. Trans. Kansas Acad. Sci., 65(2):144-153.

Tiemeier, O. W., Deyoe, C. W., and Weardon, S.
1965. Effects on growth of fingerling channel catfish of diets containing two energy and two protein levels. Trans. Kansas Acad. Sci., 68(4):379-392.

Tiemeier, O. W., and Elder, J. B.
1957. Limnology of Flint Hills farm ponds for 1956 and preliminary report on growth studies of fishes. Trans. Kansas Acad. Sci., 60(4): 379-392.

Tiemeier, O. W., and Moorman, R. B.
1957. Limnological observations on some Flint Hills farm ponds. Trans. Kansas Acad. Sci., 60(2):167-173.

Tunison, A. V., *et al.*
1939. Carbohydrate utilization by trout. Cortland Hatchery Report, 8:9-12.

1943. Carbohydrate digestion. Cortland Hatchery Report, 12:9-10.

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WILLIAM E. DUELLMAN

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A New Species of Fringe-limbed Tree Frog, Genus Hyla, from Darién, Panamá

BY

WILLIAM E. DUELLMAN

Exploration in the mountainous areas of Darién Province in eastern Panamá has revealed the presence of several previously unknown amphibians. One of the most unusual species found to date is a large fringe-limbed tree frog, which, like other fringe-limbed species, has large hands and fully webbed feet. In allusion to the fringelike dermal folds on the limbs, I propose that the new species be named

Hyla thysanota new species

Holotype.—United States National Museum No. 151080 from Cerro Malí, Darién Province, Panamá (elevation 1265 meters), obtained by Dr. Charles O. Handley, Jr., on February 11, 1964.

Diagnosis.—Size large (95.7 mm. snout-vent length); dermal fringe on outer edge of forearm and outer edge of tarsus; skin of head and dorsum granular and uniformly green.

Description of holotype.—Adult female containing ovarian eggs and having snout-vent length of 95.7 mm.; tibia length 51.0 mm., 52 per cent of snout-vent length; foot length (measured from proximal edge of inner metatarsal tubercle to tip of longest toe) 44.6 mm., 46 per cent of snout-vent length; head length 31.1 mm., 32 per cent of snout-vent length; greatest width of head just anterior to angle of jaws 36.5 mm., 36 per cent of snout-vent length; snout, in lateral profile, rounded, in dorsal profile, broadly rounded; canthus heavy, rounded; loreal region deeply concave; lips broad, flaring. Nostrils protuberant laterally; internarial distance 7.0 mm., 19 percent of head width; head flat above; interorbital distance 12.0 mm., 33 per cent of head width; width of eyelid 8.1 mm., 22 per cent of head width; diameter of eye 8.3 mm.; pupil horizontally ovoid, palpebrum unmarked; diameter of tympanum 4.8 mm., 58 per cent of eye, situated directly posterior to eye, separated from eye by 4.9 mm.; upper edge of tympanum covered by dermal fold extending posteriorly from eye to point above insertion of arm.

Upper arm short, slender; forearm only slightly robust; two transverse folds on wrist; thin, scalloped dermal fringe along outer edge of forearm from elbow to disc of fourth toe; hand large, 32.0 mm. from proximal edge of prepollex to tip of longest toe; length of fingers from shortest to longest, 1-2-4-3, fourth only slightly longer than second; fingers webbed to bases of discs, except web between first and second fingers extending only to bases of penultimate phalanges; discs large, all except that on first finger larger than tympanum; distal subarticular tubercle flat, others conical; supernumerary tubercles small, conical, present only on proximal segments, especially numerous on base of fourth

finger and on thumb, larger and fewer on second finger; prepollex elongate, flat, broadly visible from above, supported by flat bony spine; numerous small conical tubercles on ventral surface of prepollex and palm (Fig. 1a); heels overlap by about one-third length of tibia when hind limbs adpressed; tibiotarsal articulation extending to eye; distinct dermal folds on knees and heels; thin tarsal fold curving from heel to inner metatarsal tubercle; thin, scalloped dermal fringe along outer edge of foot from heel to disc of fifth toe; inner metatarsal tubercle flat, broadly elliptical, visible from above; outer metatarsal tubercle absent; length of toes from shortest to longest, 1-2-5-3-4; toes fully webbed; discs smaller than on fingers; subarticular tubercles conical; supernumerary tubercles small, conical, in one row on each proximal segment (Fig. 1b).

Anal opening directed posteriorly at level of middle of thighs; anal sheath short, granular; distinct granular dermal fold on each side of anus. Skin on top of head and body finely granular (perhaps containing osteoderms); skin on belly and median posteroventral surfaces of thighs granular; other surfaces smooth. Tongue broadly cordiform, shallowly notched posteriorly, barely free behind. Vomerine ridges transverse, narrowly separated medially, situated between round choanae; vomerine teeth, 10-11; premaxillary teeth, 15-16; maxillary teeth, 73-71; all teeth strongly spatulate and bifid.

Color (*in alcohol*): dark purplish brown on dorsal surfaces of head, body, limbs, outer three fingers, and outer two toes; lower flanks, anterior and posterior surfaces of thighs, and ventral surfaces of hind limbs pale brown; webs dark brown; belly creamy yellow with brown spots anteriorly; chin brown; upper lip grayish white. Color (*in life*, according to collector's field notes): dorsum green; ventral surfaces pinkish white; eyes brown.

Skull (skin peeled back from head permitting superficial examination of skull) broader than long; having only moderate amount of ossification—no well-developed maxillary flanges (pars facialis) nor supraorbital processes; alary processes of premaxillary high; internasal septum cartilaginous; nasals slender, separated, long axes parallel to maxillaries, anterior ends not extending beyond sphenethmoid, not forming complete bony anterior margin to orbit; sphenethmoid large, bony in entire interorbital distance, anterolateral margins attached to nasals, posterior margin overlain by frontoparietals, extending posteriorly three-quarters length of orbit; frontoparietals slender, converging medially posterior to frontoparietal fontanelle, having cartilaginous flange over posterior part of orbit; frontoparietal fontanelle ovoid, about thrice as long as wide; quadratojugal robust; squamosal having extremely short anterior arm, moderately long posterior arm, well-developed ventral arm; prevomers large, forming anterior, but not posterior, margins of choanae; palatines well developed, toothless, extending medially to sphenethmoid, lacking prepalatine processes.

Discussion.—Hyla thysanota is another species in that group of bizarre hylids usually referred to as the fringe-limbed tree frogs. In size it approaches *Hyla immensa* Taylor from Costa Rica and *H. phantasmagoria* Dunn from Colombia, but both of these species have tuberculate skin on the dorsum, shorter and more blunt snouts, relatively larger tympani, and mottled brown dorsal coloration.

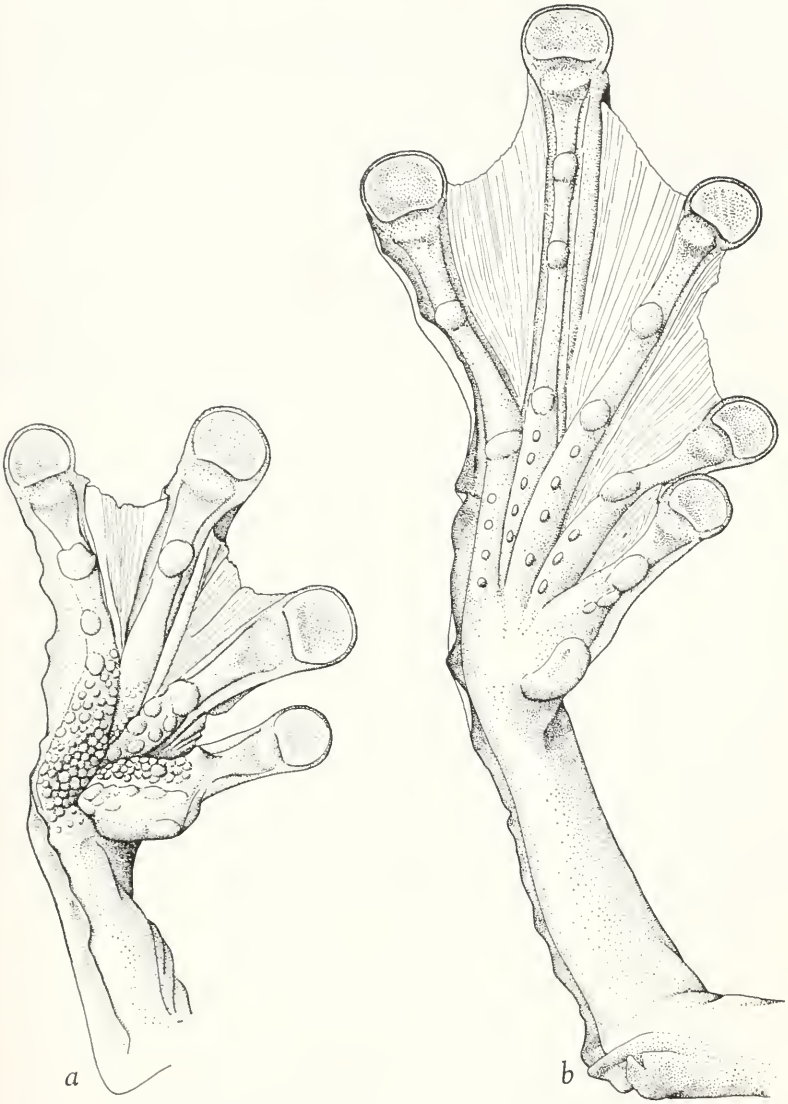

FIG. 1. Ventral views of right hand (*a*) and right foot (*b*) of holotype of *Hyla thysanota* (USNM 151080). × 2.

Hyla miliaria Cope from Nicaragua, *H. richardtaylori* Taylor and *H. fimbrimembra* Taylor from Costa Rica are smaller species having less webbing, more scalloped dermal fringes, and brown dorsal coloration. *Hyla valancifer* Firschein and Smith and *H. echinata* Duellman from México have smooth skin on the dorsum, narrower fringes on the limbs, and brown dorsal coloration. The uniformly green dorsum of *H. thysanota* is unique among the fringe-limbed hylids.

Present knowledge of the fringe-limbed hylids, of which there are nearly as many names as known specimens, is insufficient to account for relationships. Perhaps the several species are members of two or more phyletic lines. It is noteworthy that the sizes and relationship of the cranial roofing bones of *Hyla thysanota* closely resemble those in *Hyla maxima.*

The type was shot from a tree-top at night, after its eye-shine was observed. The specimen was found in humid montane forest near the headwaters of the Río Pucro (Pacific drainage via the Río Tuira) on the east slope of Cerro Malí, which lies south of Cerro Tacarcuna in the Serranía del Darién.

Acknowledgments.—In January of 1964 I was in Panamá and planned to accompany Dr. Handley to Cerro Malí. Political events delayed our departure and I had to return to the United States. Dr. Handley generously took time from his collecting of mammals to secure amphibians and reptiles. I am grateful to him for his efforts and to James A. Peters for the loan of the specimens from the United States National Museum. I am indebted to Linda Trueb for the delineation of the hands and feet reproduced here as Figure 1. This paper is one result of the author's studies on Middle American hylid frogs supported by a grant from the National Science Foundation (NSF GB-1441) and a part of a survey of the herpetofauna of Panamá supported by a grant from the National Institutes of Health (NIH GB-12020).

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Taxonomic Notes on Some Mexican and Central American Hylid Frogs

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Taxonomic Notes on Some Mexican and Central American Hylid Frogs

BY

WILLIAM E. DUELLMAN

The acquisition of series of many species of hylid frogs from México and Central America and the comparison of these specimens with the types of many named taxa have provided the basis for certain taxonomic conclusions. The purpose of this paper is to comment on certain species and to make necessary nomenclatural changes. In this report, eleven taxa are placed in the synonymy of nine others, one previously recognized species is regarded as a subspecies, and one species is placed in a different genus. The genera and species, as now recognized, are treated in alphabetical order.

The abbreviations used for the various collections are: AMNH (American Museum of Natural History), CNHM (Chicago Natural History Museum), FAS (Frederick A. Shannon collection), KU (University of Kansas Museum of Natural History), MCZ (Museum of Comparative Zoology), RCT (Richard C. Taylor collection), UMMZ (University of Michigan Museum of Zoology), and USNM (United States National Museum).

For the loan of specimens or for permitting me to work in their respective institutions, I am grateful to Charles M. Bogert, Doris M. Cochran, Robert F. Inger, Edmund Malnate, Jay M. Savage, the late Frederick A. Shannon, Hobart M. Smith, Charles F. Walker, Ernest E. Williams, and Richard G. Zweifel. This paper is a result of research on Middle American hylid frogs supported by the National Science Foundation (Grant No. GB-1441).

Gastrotheca ceratophrys (Stejneger) New combination

Hyla ceratophrys Stejneger, Proc. U. S. Natl. Mus., 41:286, August 14, 1911 [Holotype.—USNM 47705, Upper Río Pequeni, Panamá Province, Panamá; A. H. Jennings collector].

This large and distinctive species heretofore has been known only from the holotype. The acquisition of three additional specimens, one a female carrying nine eggs, confirms a suspicion that the species belongs in the genus *Gastrotheca.* I have examined USNM 141795 from Tacarcuna, Darién, KU 77016 from Laguna,

Darién, KU 95794 from 5 kilometers west of Almirante, Bocas del Toro, Panamá, and the holotype. Three males have snout-vent lengths of 68, 72, and 74 mm., and the female (KU 77016) has a snout-vent length of 71 mm. The specimens are alike in having only a vestige of a web between the fingers and in having the toes webbed to the bases of the discs, except the fourth toe, which is webbed to the base of the antepenultimate phalanx. The anal opening is directed posteriorly at the level of the upper surfaces of the thighs. Contrary to the statement by Stejneger (1911:286), the skin on the head is not co-ossified with the underlying cranial bones. There are seven to nine transverse rows of minute tubercles on the dorsum of the head and body. The outer edge of the upper eyelid projects in the form of a triangular "horn," which is pointed in three specimens, but terminally notched in KU 95794.

Males are tan on the dorsum with darker brown transverse bands of varying widths (diffuse in USNM 141795) and have narrow brownish-black transverse stripes on the limbs. The belly is creamy white. The female is much darker than the males and has a dark brown dorsum, darkest laterally; the limbs are brown with dark brown transverse markings; the ventral surfaces are grayish tan. All specimens have a small white spot on each side ventrolateral to the anal opening and a pale bar extending from the orbit to the lip; in the female this bar is an enamellike white, whereas in the others the bar is creamy tan.

In life the female was pale tan when found at night; by day she changed to dull brown above and creamy-tan below with pale orange-tan thighs. The subocular bar, labial flecks, and subanal spots were white, and the iris was a dull bronze-color. The male from five kilometers west of Almirante had an olive-tan dorsum with brown transverse markings; the limbs were yellowish tan above with grayish brown bands, and the webs and flanks were yellowish tan. The upper lip was barred with olive-tan and brown; the venter was white, and the iris was a coppery bronze-color medially and a golden bronze-color peripherally.

Gastrotheca cornutum (Boulenger, 1898:124), which occurs on the Pacific slopes of Eucador and Colombia, has superciliary triangular appendages like those in *G. ceratophrys*. Perhaps the two are conspecific, but on the basis of the limited number of specimens and the lack of an opportunity to examine the holotype of *G. cornutum*, I tentatively retain *G. ceratophrys* as a species.

Hyla colymba Dunn

Hyla colymba Dunn, Occas. Pap. Boston Soc. Nat. Hist., 5:400, August 18, 1931 [Holotype.—MCZ 10234, La Loma, Bocas del Toro Province, Panamá; Chester Duryea and E. R. Dunn collectors].

Hyla alvaradoi Taylor, Univ. Kansas Sci. Bull., 35:882, July 1, 1952 [Holotype.—KU 30886, Moravia, Cartago Province, Costa Rica; Edward H. Taylor collector].

Dunn (1924:3) originally reported this species from La Loma as *Hyla albomarginata* Spix; his specimens later formed the type series of *Hyla colymba* (Dunn, 1931a:400) and were compared with *Hyla albomarginata.* The hototype and an adult paratype each possesses a circular mental gland encompassing most of the anterior edge of the chin; this gland was not mentioned by Dunn. Taylor (1952:882) based the description of *Hyla alvaradoi* on one adult male and subsequently (1954:625) reported two additional specimens from the type locality. Taylor (1952:882) gave a detailed description of the type of *Hyla alvaradoi,* and he noted the circular mental gland, but he did not compare *Hyla alvaradoi* with *H. colymba.*

Comparison of the holotypes of *H. alvaradoi* and *H. colymba* shows that the two specimens are nearly identical in structure; the former has fewer supernumerary tubercles on the hand than the latter, but a paratype of *H. colymba* (MCZ 10235) has as many supernumerary tubercles as the holotype of *H. alvaradoi.* The coloration of the types of the two alleged species and other specimens examined agrees and is distinctive. Although in life, the frogs are greenish yellow above, in preservative they fade to a creamy white with chromatophores forming flecks, or clusters, on the dorsum, especially anteriorly. A white or yellowish-white line from the canthus along the outer edge of the eyelid to a point above the insertion of the arm is a diagnostic feature of this species.

Hyla colymba ranges from low to moderate elevations on the Caribbean lowlands of Costa Rica to the Serranía del Darién in extreme eastern Panamá. I have examined specimens from La Lola and Moravia in Costa Rica and from the following localities in Panamá: La Loma, Chiriquí Province; El Valle, Coclé Province; Altos de Pacora, Panamá Province, and Laguna and Cerro Malí, Darién Province.

Hyla ebraccata Cope

Hyla ebraccata Cope, Proc. Acad. Nat. Sci. Philadelaphia, 26:69, 1874 [Holotype.—unknown, Nicaragua; John F. Bransford collector].

Hyla weyerae Taylor, Univ. Kansas Sci. Bull., 36:633, June 1, 1954 [Holotype.—KU 34850, Esquinas Forest Preserve, Las Esquinas, between

Palmar and Golfito, Puntarenas Province, Costa Rica; Mrs. Albert E. Weyer collector].

In his description of *Hyla weyerae* Taylor (1954:635) did not compare the frog with *Hyla ebraccata,* but instead stated: "This small species may belong in a group of small frogs that includes *Hyla alleei, Hyla rufiocula* (sic), and *Hyla uranochroa.* . . ." There are no morphological characters to associate *Hyla weyerae* with *H. uranochroa* and its allies, but there exist no morphological characters by which to separate the holotype of *H. weyerae* from *H. ebraccata.* All individuals of the latter are like the type of *H. weyerae* in possessing an extensive axillary membrane, white labial stripe expanded below the eye, and unpigmented thighs. Most specimens (462 of 549 examined from Middle America) have a dorsal dark-mark roughly in the form of an hour-glass. The holotype of *H. weyerae* differs by lacking any dorsal markings.

Examination of series of specimens from throughout the range of the species reveals the presence of plain (unmarked) individuals from several localities, but they always are in the minority as compare with individuals having the hour-glass mark on the back. Some individuals lack the hour-glass mark but have small dark brown spots on the dorsum; some specimens from the northern part of the range have the hour-glass mark fragmented into an anterior triangular mark and one or two spots in the sacral region (Table 1). The highest incidence of plain individuals is in the Palmar-Golfito area of Costa Rica (including the type locality of *H. weyerae*), where six of 13 specimens have no dorsal markings.

I have collected plain and "normal" individuals from the same pond on the same night and can discern no differences in the breeding call. These observations and the occurrence of plain individuals at several localities on both Caribbean and Pacific lowlands of Central America indicate that the name *Hyla weyerae* is based on a color variant of *Hyla ebraccata.*

Dunn (1931b:407, 1933:63) and Breder (1946:417) used the name *Hyla leucophyllata* (Beireis) for Panamanian frogs currently assigned to this species. Likewise, Taylor (1942:80) used that name for specimens from Piedras Negras, Guatemala. I am now convinced that all known specimens from México and Central America are *H. ebraccata,* which ranges into northern Colombia and differs from *H. leucophyllata* in having a white labial mark expanded below the eye. The lips of *H. leucophyllata* are uniform brown.

TABLE 1.—COLOR PATTERN VARIANTS IN HYLA EBRACCATA

Locality	Hour-glass	Triangle	Spotted	Plain	Total
Valle Nacional, Oaxaca, México	19	—	—	—	19
Teapa, Tabasco, México	13	2	—	1	16
Toocog, El Petén, Guatemala	47	6	—	—	53
Turrialba, Cartago, Costa Rica	87	—	—	—	87
Pacuare, Cartago, Costa Rica	48	—	—	—	48
Moravia, Cartago, Costa Rica	21	—	—	—	21
Suretka, Limón, Costa Rica	45	—	6	14	65
Tilarán, Guanacaste, Costa Rica	50	—	3	15	68
Palmar—Golfito, Puntarenas Costa Rica	7	—	—	6	13
Anchiote, Colón, Panamá	46	—	16	15	77
Cerro la Campana, Panamá, Panamá	16	—	3	—	19
Tacarcuna-Río Mono, Darién, Panamá	63	—	—	—	63
Totals	462	8	28	51	549

Several species in the *Hyla leucophyllata* group in the upper Amazon Basin (*H. bifurca, frontalis, laynei, membranacea, reticulata, rossalleni,* and *sarayacuensis*) differ only in minor features of the color pattern. *Hyla membranacea* is an unmarked species colored like the holotype of *H. weyerae,* and *Hyla laynei* is spotted much like many individuals of *H. ebraccata.* The evidence presented here concerning variation in color-pattern in *Hyla ebraccata* suggests that detailed studies of living frogs and series of specimens of the *Hyla leucophyllata* group in the upper Amazon Basin might reveal an unwarranted multiplicity of named taxa.

Hyla elaeochroa Cope

Hyla elaeochroa Cope, Jour. Acad. Nat. Sci. Philadelphia, ser. 2, 8:105, 1876 [Lectotype.—USNM 30689, east foot of mountains near Sipurio, Limón Province, Costa Rica; William M. Gabb collector].

Hyla quinquevittata Cope, Proc. Amer. Philos. Soc., 23:273, April 1886 [Holotype.—USNM 14187, Nicaragua; J. F. Bransford collector].

Hyla dulcensis Taylor, Univ. Kansas Sci. Bull., 39:37, November 18, 1958 [Holotype.—KU 32168, Golfito, Puntarenas Province, Costa Rica; Edward H. Taylor collector].

Dunn and Emlen (1932:25) placed *H. elaeochroa* and *H. quinquevittata* as synonyms of *H. rubra*. Taylor (1952:861) concurred that *H. elaeochroa* and *H. quinquevittata* were conspecific but thought that *Hyla rubra* was another species. Taylor (1958:37) described *Hyla dulcensis* from Golfito on the Pacific lowlands of Costa Rica; he diagnosed the new species (based on two males and one female) as differing from *H. elaeochroa* on the Caribbean lowlands in having "somewhat larger size, smaller finger and toe discs, the obsolete canthus rostralis, the loreal region concave, and the choanae larger."

Examination of several series of specimens from Costa Rica and Panamá reveals that individuals from the Golfo Dulce area on the Pacific lowlands of Costa Rica attain a slightly larger size than do the frogs elsewhere in the range of the species, but that the difference is minor. For example, fifteen males chosen at random from each of three localities in Costa Rica vary in snout-vent length as follows: Golfo Dulce area, Puntarenas Province 33.8 (29.6-38.8 mm.); Puerto Viejo, Heredia Province 29.6 (27.9-32.3 mm.); Turrialba, Cartago Province 30.5 (27.9-32.6 mm.). Sixteen males (including the holotype) from the Golfo Dulce region display variation in the canthus, loreal region, size of discs on digits and size of choanae that extends from the condition described in *H. dulcensis* to that ordinarily found in *H. elaeochroa* on the Caribbean lowlands. The nearly identical breeding calls, close resemblance of tadpoles, and lack of any definitive morphological criteria indicate that *Hyla dulcensis* Taylor is a synonym of *H. elaeochroa* Cope.

Until Taylor named *Hyla dulcensis, Hyla elaeochroa* was not known from the Pacific coast of Central America. Subsequent collecting has extended the known range of *H. elaeochroa* westward through the Arenal depression in Guanacaste and southward along the Pacific slopes to the Golfo Dulce area.

Dunn and Emlen (1932:25) incorrectly placed *H. elaeochroa* in the synonymy of *H. rubra*. The former has no pattern on the posterior surfaces of the thighs, whereas the bold black and creamy

yellow pattern is present in *H. rubra.* A gap of about 225 kilometers separates the known ranges of the two species. *Hyla elaeochroa* ranges from east-central Nicaragua southward to the Golfo Dulce area of Costa Rica and on the Caribbean lowlands to Laguna de Chiriquí in western Panamá, whereas *Hyla rubra* is widespread in South America, but in Panamá ranges no farther west than the Canal Zone.

Hyla lancasteri Barbour

Hyla lancasteri Barbour, Proc. New England Zool. Club., 10:31, Pl. 4, fig. 2, March 2, 1928 [Holotype.—MCZ 13062, Peralta, Cartago Province, Costa Rica; C. R. Lancaster collector].

Hyla moraviaensis Taylor, Univ. Kansas Sci. Bull., 35:865, fig. 57, July 1, 1952 [Holotype.—KU 30284, Moravia, Cartago Province, Costa Rica; Edward H. Taylor collector].

Barbour (1928:31) named *Hyla lancasteri* on the basis of one juvenile having a snout-vent length of 19.1 mm. Dunn and Emlen (1932:25) placed *H. lancasteri* in the synonymy of *H. boulengeri.* Taylor (1952:858) questioned that allocation of *H. lancasteri.* A comparison of the holotypes of *H. lancasteri* and *H. moraviaensis* with well-preserved specimens of *H. boulengeri* (including juveniles) reveals that the latter is specifically distinct from both *H. lancasteri* and *H. moraviaensis,* but that the holotype of *H. lancasteri* is conspecific with the frogs that Taylor (1952:865) named *Hyla moraviaensis.* Although the type of *H. lancasteri* is in poor condition and the only markings present are the dark bars on the hind limbs, the species can be associated with *H. moraviaensis* by the broad head, short truncate snout, short fingers, and amount of webbing. In all of these characters *H. lancasteri* differs notably from *H. boulengeri,* which has a relatively narrow head, long pointed snout, and relatively long fingers. Dunn and Emlen (1932:25) apparently synonymized *H. lancasteri* with *H. boulengeri* solely on the basis of the strongly barred thighs, a coloration known at that time, in Central American hylids, only in *H. boulengeri.*

Although many specimens of *Hyla lancasteri* are in collections, all are from the Caribbean slopes of Cartago Province, Costa Rica.

Hyla loquax Gaige and Stuart

Hyla loquax Gaige and Stuart, Occas. Pap. Mus. Zool. Univ. Michigan, 281:1, June 9, 1934 [Holotype.—UMMZ 75446, Ixpuc Aguada, north of La Libertad, Departamento El Petén, Guatemala; L. C. Stuart collector].

Hyla stadelmani Schmidt, Proc. Biol. Soc. Washington, 49:45, May 1, 1936 [Holotype.—MCZ 21310, Subirana Valley, Departamento Yoro, Honduras; Raymond E. Stadelman collector.]

Hyla axillamembrana Shannon and Werler, Trans. Kansas Acad. Sci., 58:383, fig. 6, September 24, 1955 [Holotype.—FAS 4083, 5 mi. south of Lake Catemaco on San Andrés Tuxtla-Minatitlán road, Veracruz, México; John Werler and Jack Reid collectors].

Hyla loquax is one of the most distinctive Middle American tree frogs; in living and freshly preserved specimens the thighs and webs are red, but in old preserved specimens the red fades to creamy white. Gaige and Stuart's (1934:2) description included an account of the coloration of living frogs (collected and observed by Stuart), but Schmidt (1936:45) had no acquaintance with the frogs in life that he named *Hyla stadelmani.*

I have compared the type and a paratype of *H. stadelmani* (MCZ 21310-11) with two paratypes of *H. loquax* (MCZ 19754, 21456) and several other specimens of *H. loquax* from Central American and southern México. These specimens obviously represent one taxon. The older preserved specimens of *H. stadelmani* and *H. loquax,* from which the colors have faded, are indistinguishable.

Duellman (1960:62) placed *Hyla axillamembrana* in the synonymy of *Hyla loquax,* which is widely distributed in the forested Gulf and Caribbean lowlands from southern Veracruz to Costa Rica.

Hyla melanomma bivocata Duellman and Hoyt, new combination

Hyla bivocata Duellman and Hoyt, Copeia, no. 4:414, figs. 1-3, December 19, 1961 [Holotype.—KU 58446, stream above (6.2 kilometers by road south of) Rayón Mescalapa, Chiapas, México; William E. Duellman and Dale L. Hoyt collectors].

Examination of specimens of *Hyla melanomma* (Taylor, 1940) and the acquisition of specimens from the Mexican state of Oaxaca provide evidence of close relationship of *H. bivocata* to *H. melanomma.* Both are small (snout-vent lengths of breeding males 26.1-29.9 mm.), yellowish-tan frogs having axillary membranes, acuminate snouts in dorsal view, and breeding calls consisting of a primary note followed by shorter secondary notes. These resemblances notwithstanding, certain differences exist between the frogs in the Chiapan highlands and those in the Mexican highlands west of the Isthmus of Tehuantepec. The most noticeable difference between *H. bivocata* from Chiapas and *H. melanomma* from Guerrero and Oaxaca is the much smaller tympanum of the former. Seven males of *H. bivocata* from above Rayón Mescalapa, Chiapas, have tympanum/eye ratios of 0.276-0.323 (mean 0.298), whereas the ratio in three samples of *H. melanomma* is higher—eight males from Agua del Obispo, Guerrero, 0.500-0.531 (0.514), seven from 12 kilometers north-northwest of San Gabriel Mixtepec on the Pacific

slopes of Oaxaca, 0.478-0.550 (0.511), and two from Campamento Vista Hermosa on the Atlantic slopes of Oaxaca, 0.368-0.419 (0.394). Aside from this measurable difference, the Chiapan frogs have slightly less webbing on the hands and fewer dark flecks on the dorsal surfaces, especially on the shanks, as compared with those specimens from Oaxaca and Guerrero.

Subspecific recognition of the populations seems to be warranted. Thus, *Hyla bivocata* Duellman and Hoyt becomes *Hyla melanomma bivocata*. It is known only from the northern slopes of the highlands of Chiapas, whereas *H. m. melanomma* occurs on the coastal slopes of the Sierra Madre del Sur in Guerrero and Oaxaca. Four specimens (KU 87112-5) are from Campamento Vista Hermosa on the northern slopes of the Sierra de Juárez in northern Oaxaca. The two adult males are intermediate between *H. m. bivocata* and *H. m. melanomma* in respect to the size of the tympanum relative to the eye, but in other characters are more nearly like *H. m. melanomma*.

Hyla pictipes Cope

Hyla punctariola pictipes Cope, Jour. Acad. Nat. Sci. Philadelphia, ser. 2, 8:106, 1876 [Syntypes.—USNM 30631, 30652, Pico Blanco, Limón Province, Costa Rica; W. M. Gabb collector].

Hyla punctariola moesta Cope, Jour. Acad. Nat. Sci. Philadelphia, ser. 2, 8:106, 1876 [Holotype.—USNM 30660, Pico Blanco, Limón Rov Province, Costa Rica; W. M. Gabb collcetor].

Hyla punctariola monticola Cope, Jour. Acad. Nat. Sci. Philadelphia, ser. 2, 8:106, 1876 [Holotype.—USNM 30661, Pico Blanco, Limón Province, Costa Rica; W. M. Gabb collector].

Cope (1876:106) erroneously associated his specimens of hylids with Peter's *Hyla punctariola*, which actually is an *Eleutherodactylus* (Dunn, 1940:109). Taylor (1952:855, 878) is the only worker who subsequently treated these names, and he placed each as a distinct species of *Hyla*, although he had no new material and had not examined the types of *H. moesta* or *monticola*.

In April, 1964, Jay M. Savage and I examined the types of the three subspecies described by Cope in an attempt to determine which names, if any, were applicable to various hylids that we had collected in the highlands of Costa Rica. All four types are soft, badly faded, and partially deteriorated, thereby making accurate comparisons and determinations impossible. We were unable to distinguish these types from one another by any seemingly meaningful character and agreed that the differences observed in the types were encompassed in the range of variation displayed by series of a species that we had collected in Costa Rica. The names

and descriptions of all three taxa appear on the same page (Cope, 1876:106). The name that appeared first on the page is here chosen. *Hyla punctariola moesta* and *H. p. monticola* are relegated to the synonymy of *Hyla pictipes*.

Since this species have never been adequately described, the following description (based on KU 64643-87 from Río Poasito, Alajuela Province, Coast Rica) is provided: snout-vent length of 10 males 34.6 (32.0-36.7 mm.), of six females 42.2 (40.6-43.2 mm.); tibia slightly longer than half snout-vent length; snout truncate viewed laterally and acuminate viewed dorsally; top of head flat; diameter of tympanum about half diameter of eye; fingers long, stout, about one-fourth webbed; toes short, about two-thirds webbed; inner metatarsal tubercle elevated, flat, elliptical; outer metatarsal tubercle smaller, conical; tarsal fold lacking; palms, soles, ventral surfaces of proximal segments of digits bearing numerous conical supernumerary tubercles; anal sheath short; anal opening at level of middle of thighs, directed ventrally; skin or dorsum and limbs smooth; skin or belly granular.

The coloration of preserved specimens is dull brown or tan on dorsal surfaces of females and either uniform dark brown or dull brown with many darker spots dorsally in males. In females the flanks and anterior and posterior surfaces of the thighs are tan with cream-colored spots, whereas in males these surfaces are dark brown or black with smaller cream-colored spots. The ventral surfaces are creamy gray with moderate (usually in females) or heavy (usually in males) suffusion of dark brown.

In life, males have an olive-green dorsum with dark olive-green or brown spots; in females the dorsum is uniform pale green. Individuals of both sexes have brown flanks and thighs with yellow spots and a golden tan iris.

This stream-breeding *Hyla* occurs at elevations above 1500 meters in the Cordillera Central and in the Cordillera de Talamanca in Costa Rica.

Hyla staufferi Cope

Hyla staufferi Cope, Proc. Acad. Nat. Sci. Philadelphia, 17:195, October 1865 [Holotype.—USNM 15317, Orizaba, Veracruz, México; Francis Sumichrast collector].

Hyla culex Dunn and Emlen, Proc. Acad. Nat. Sci. Philadelphia, 84-24, March 22, 1932 [Holotype.—MCZ 16098, Tela, Departamento Atlantidad, Honduras; Raymond E. Stadelman collector].

Hyla altae Dunn, Occas. Papers Boston Soc. Nat. Hist., 8:61, June 7, 1933. [Holotype.—MCZ 17972, Summit, Canal Zone, Panamá].

After comparing the types of the three proposed names with series of well-preserved specimens from throughout the range of the species, I concur with Taylor (1952:865) that only one species is involved. *Hyla culex* was named and described on the basis of an adult male having a snout-vent length of 25.1 mm. In his key to the species of the *Hyla rubra* group in Central America, Dunn (1933:62) separated *Hyla culex* from other members of the group by the former having a tympanum that was one-third the size of

the eye; in the other recognized taxa the tympanum is larger. Examination of series of *Hyla staufferi* from throughout the range of the species reveals that the size of the tympanum is variable, and that the frogs in northern Honduras do not differ significantly from individuals from other parts of the range. In the description of the type, Dunn and Emlen (1932:24) mentioned the presence of a dark interorbital triangle, dorsolateral marks, and transverse dark marks on the limbs, but Dunn (1933:62) stated that *H. culex* lacked stripes. The holotype of *H. culex* is soft and faded, but dark dorsolateral stripes, a canthal stripe, and transverse marks on the limbs are faintly visible.

Dunn (1933:61) named *Hyla altae* on the basis of five males obtained at Summit, Canal Zone, Panamá, and compared these specimens with *Hyla rubra* and *boulengeri.* The holotype of *H. altae* is indistinguishable from individuals of *Hyla staufferi,* which lack dark transverse marks on the limbs. The pattern on the dorsal surfaces of the hind limbs varies from unicolor grayish tan to a pattern involving numerous dark flecks, a dark longitudinal stripe, or one or two dark transverse marks. Unicolor hind limbs are more prevalent in Panamá and Costa Rica than in other parts of the range.

The taxonomy of *Hyla staufferi* has been confused for many years. Cope (1887:14) placed *H. staufferi* as a subspecies of *H. eximia.* Günther (1901:262) considered *H. staufferi* to be a synonym of *H. eximia.* Gaige (1936:293) suggested that *H. culex* and *H. altae* might be conspecific, but regarded *H. staufferi* as a different species, although she correctly intimated that *H. staufferi* belonged in the *rubra* group and not with *H. eximia.* The only subsequent departure from this arrangement was that of Blair (1960), who placed *H. staufferi* in the *eximia* group on the basis of the similarity in breeding calls.

Skeletal features, especially the characteristics of the broad nasals and slender tegmen tympani, the body form of the tadpoles, and the absence of webbing between the first and second toes are some of the more significant characters that indicate relationships of *Hyla staufferi* with the *Hyla rubra* group. *Hyla staufferi* is the northernmost species in the group, which is predominately South American; *H. staufferi* ranges from Guerrero and southern Tamaulipas, México southeastward to the Bayano Valley of east-central Panamá at low and moderate elevations throughout Central America, exclusive of the wet tropical forests of the Caribbean lowlands.

Hyla uranochroa Cope

Hyla uranochroa Cope, Jour. Acad. Nat. Sci. Philadelphia, ser. 2, 8: 103, pl. 27, fig. 4, 1876 [Holotype.—USNM 30651, near Sipurio, Limón Province, Costa Rica; W. M. Gabb collector].

Hyla alleei Taylor, Univ. Kansas Sci. Bull., 35:831, fig. 48, July 1, 1952 [Holotype.—RCT 775, Isla Bonita, Heredia Province, Costa Rica; Richard C. Taylor collector].

Taylor (1952:837) examined the holotype of *H. uranochroa* and MCZ 10249 from La Loma, Panamá, but referred two specimens from Isla Bonita to a new species, *Hyla alleei,* which he distinguished from *H. uranochroa* on the basis of (1) lacking a white stripe above the anus, (2) having the diameter of the tympanum about one-half that of the eye (larger in *H. uranochroa*), (3) having only a vestige of web on hand (outer-fingers one-fourth webbed in *H. uranochroa*), and (4) lacking a distinct inner tarsal fold (moderately distinct in *H. uranochroa*). I have examined 139 specimens from Costa Rica and western Panamá, including the holotype of *H. uranochroa* and the paratype of *H. alleei* (CNHM 101375, formerly RCT 774). Of 20 specimens from the type locality, only four lack a white stripe above the anus; six of 15 from Moravia, Cartago Province, Costa Rica, apparently lack the white stripe. The nature of the tarsal fold is variable; in some individuals the fold is lacking and in others it is weak. In those specimens having a better developed tarsal fold, the fold is weak and extends only about half the length of the tarsus. The amount of webbing in the hand is slight; in no specimen are the fingers more than one-fourth webbed and some specimens have only a vestigial web between the outer fingers. The diameter of the tympanum of most specimens is 60 to 65 per cent of the diameter of the eye; I have seen no specimens having a tympanum/eye ratio of less than 53 per cent.

The absence of distinguishing characters of morphology and coloration together with the presence of only one kind of breeding call and one kind of tadpole is indicative of the presence of only one species. *Hyla uranochroa* is a distinctive stream-breeding frog living at elevations usually above 1100 meters, although in Costa Rica, individuals have been found at 650 meters at Ciudad Quesada, Alajuela Province and at 680 meters at El Tigre, Limón Province. The species occurs on the Caribbean and Pacific slopes of Costa Rica and is known from La Loma on the Caribbean slopes of western Panamá.

Hyla uranochroa is the only member of the genus in Central America having a bright green dorsum, creamy-yellow belly, white lateral stripe, and bright red eye. Two other apparently related, red-eyed species (*H. legleri* and *H. rufioculis*) differ in having dark olive-green or brown dorsal colors and noticeably different breeding calls.

Phrynohyas spilomma (Cope)

Hyla spilomma Cope, Proc. Amer. Philos. Soc., 17:86, August 1877 [Holotype.—unknown, Cosamaloapam, Veracruz, México; Francis Sumichrast collector].

Acrodytes modesta Taylor and Smith, Proc. U. S. Natl. Mus., 95:594, pl. 27, fig. 2, pl. 28, figs. 2-3, June 30, 1945 [Holotype.—USNM 115013, Cruz de Piedra, near Acacoyagua, Chiapas, México; Dr. and Mrs. Hobart M. Smith collectors].

In his revision of *Phrynohyas*, Duellman (1956) regarded *P. spilomma* and *P. modesta* as distinct species. The former was characterized by an irregular dorsal dark mark and distinct dark transverse bands on the limbs, whereas *P. modesta* was characterized by the absence of any dorsal markings, except scattered black spots. In 1956 *P. modesta* was known from eight localities in southern Veracruz and the Pacific lowlands of Chiapas, Guatemala, and El Salvador. Fugler (1960:10) reported *P. modesta* from British Honduras, and Neill (1965:88) noted that the color pattern in *Phrynohyas* from British Honduras varied from the nearly unicolor pattern of *P. modesta* to the pattern described for *P. spilomma*.

Examination of specimens of *Phrynohyas* collected since 1956 reveals two additional specimens from Veracruz, 19 specimens from Tabasco, and one from Honduras, in addition to those reported from British Honduras. Seventy-two specimens (AMNH 74377-90) from Cuyuta, 20 kilometers north of San José, Departamento Escuintla, Guatemala, show a range in variation encompassing that previously known in both *P. spilomma* and *P. modesta*. Some specimens in the series have a unicolored tan dorsum; in others the tips of the warts are dark brown. Some specimens have dark brown dorsolateral bands, and in others the mid-dorsal region also is dark brown. Therefore, it seems that the uniform tan dorsum is only an extreme, but common and widespread, color variant of *Phrynohyas spilomma*.

This intraspecific variation in coloration is like that noted in Amazonian *P. venulosa* by Duellman (1956:39).

LITERATURE CITED

Barbour, T.
1928. New Central American frogs. Proc. New England Zool. Club, 10:25-31, pls. 1-4, March 2.

Blair, W. F.
1960. Mating call as evidence of relations in the *Hyla eximia* group. Southwest. Nat., 5:129-135, November 1.

Boulenger, G. A.
1898. An account of the reptiles and batrachians collected by Mr. W. F. H. Rosenberg in western Ecuador. Proc. Zool. Soc. London, 1898: 107-126, pls. 10-18, June 1.

Breder, C. M., Jr.
1946. Amphibians and reptiles of the Rio Chucunaque Drainage, Darien, Panama, with notes on their life histories and habits. Bull. Amer. Mus. Nat. Hist., 86:375-436, pls. 42-60, August 26.

Cope, E. D.
1876. On the Batrachia and Reptilia of Costa Rica. Jour. Acad. Nat. Sci. Philadelphia, ser. 2, 8:93-154, pls. 23-28.
1887. Catalogue of batrachians and reptiles of Central America and Mexico. Bull. U. S. Natl. Mus., 32:1-98.

Duellman, W. E.
1956. The frogs of the hylid genus *Phrynohyas* Fitzinger, 1843. Misc. Publ. Mus. Zool. Univ. Michigan, 96:1-47, pls. 1-6, February 21.
1960. A distributional study of the amphibians of the Isthmus of Tehuantepec, México. Univ. Kansas Publ. Mus. Nat. Hist., 13:19-72, pls. 1-8, August 16.

Dunn, E. R.
1924. Some Panamanian frogs. Occ. Papers Mus. Zool. Univ. Michigan, 151:1-12, pls. 1-2, July 1.
1931a. New frogs from Panama and Costa Rica. Occ. Papers Boston Soc. Nat. Hist., 5:385-401, August 18.
1931b. The amphibians of Barro Colorado Island. Occ. Papers Boston Soc. Nat. Hist., 5:403-421, October 10.
1933. A new Hyla from the Panama Canal Zone. Occ. Papers Boston Soc. Nat. Hist., 8:61-64, June 7.
1940. New and noteworthy herpetological material from Panama. Proc. Acad. Nat. Sci. Philadelphia, 92:105-122, pl. 2, November 18.

Dunn, E. R., and Emlen, J. T., Jr.
1932. Reptiles and amphibians from Honduras. Proc. Acad. Nat. Sci. Philadelphia, 84:21-32, March 22.

Fugler, C. M.
1960. New herpetological records for British Honduras. Texas Jour. Sci., 12:8-13.

Gaige, H. T.
1936. Some reptiles and amphibians from Yucatan and Campeche, Mexico. Carnegie Inst. Washington Publ. 457:289-304, February 5.

Gaige, H. T. and Stuart, L. C.
1934. A new *Hyla* from Guatemala. Occ. Papers Mus. Zool. Univ. Michigan, 281:1-3, June 9.

Günther, A. C. L. G.
1885-1902. Biologia Centrali-Americana. Reptilia and Batrachia. Taylor and Francis, London, xx + 326 pp., 76 pls.

NEILL, W. T.
1965. New and noteworthy amphibians and reptiles from British Honduras. Bull. Florida State Mus., 9:77-130, April 9.

SCHMIDT, K. P.
1936. New amphibians and reptiles from Honduras in the Museum of Comparative Zoology. Proc. Biol. Soc. Washington, 49:43-50, May 1.

STEJNEGER, L.
1911. Descriptions of three new batrachians from Costa Rica and Panama. Proc. U. S. Natl. Mus., 41:285-288, August 14.

TAYLOR, E. H.
1940. Herpetological Miscellany. Univ. Kansas Sci. Bull., 26:489-571, November 27.
1942. New tailless Amphibia from Mexico. Univ. Kansas Sci. Bull., 28:67-89, May 15.
1952. A review of the frogs and toads of Costa Rica. Univ. Kansas Sci. Bull., 35:577-942, July 1.
1954. Additions to the known herpetological fauna of Costa Rica with comments on other species. No. I. Univ. Kansas Sci. Bull., 36:597-639, June 1.
1958. Additions to the known herpetological fauna of Costa Rica with comments on other species. No. III. Univ. Kansas Sci. Bull., 39:3-40, November 18.

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Neotropical Hylid Frogs, Genus Smilisca

BY

WILLIAM E. DUELLMAN AND LINDA TRUEB

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INTRODUCTION

The family Hylidae, as currently recognized, is composed of about 34 genera and more than 400 species. Most genera (30) and about 350 species live in the American tropics. *Hyla* and 10 other genera inhabit Central America; four of those 10 genera (*Gastrotheca, Hemiphractus, Phrynohyas,* and *Phyllomedusa*) are widely distributed in South America. The other six genera are either restricted to Central America or have their greatest differentiation there. *Plectrohyla* and *Ptychohyla* inhabit streams in the highlands of southern Mexico and northern Central America; *Diaglena* and *Triprion* are casque-headed inhabitants of arid regions in México and northern Central America. *Anotheca* is a tree-hole breeder in cloud forests in Middle America. The genus *Smilisca* is the most widespread geographically and diverse ecologically of the Central American genera.

The definition of genera in the family Hylidae is difficult owing to the vast array of species, most of which are poorly known as regards their osteology, colors in life, and modes of life history. The genera *Diaglena, Triprion, Tetraprion, Osteocephalus, Trachycephalus, Aparasphenodon, Corythomantis, Hemiphractus, Pternohyla,* and *Anotheca* have been recognized as distinct from one another and from the genus *Hyla* on the basis of various modifications of dermal bones of the cranium. *Phyllomedusa* is recognized on the basis of a vertical pupil and opposable thumb; *Plectrohyla* is characterized by the presence of a bony prepollex and the absence of a quadratojugal. *Gastrotheca* is distinguished from other hylids by the presence of a pouch in the back of females. A pair of lateral vocal sacs behind the angles of the jaws and the well-developed dermal glands were used by Duellman (1956) to distinguish *Phrynohyas* from *Hyla.* He (1963a) cited the ventrolateral glands in breeding males as diagnostic of *Ptychohyla.* Some species groups within the vaguely defined genus *Hyla* have equally distinctive characters. The *Hyla septentrionalis* group is characterized by a casque-head, not much different from that in the genus *Osteocephalus* (Trueb, MS). Males in the *Hyla maxima* group have a protruding bony prepollex like that characteristically found in *Plectrohyla.*

Ontogenetic development, osteology, breeding call, behavior, and ecology are important in the recognition of species. By utilizing

the combination of many morphological and biological factors, the genus *Smilisca* can be defined reasonably well as a natural, phyletic assemblage of species. Because the wealth of data pertaining to the morphology and biology of *Smilisca* is lacking for most other tree frogs in Middle America it is not possible at present to compare *Smilisca* with related groups in more than a general way.

Smilisca is an excellent example of an Autochthonous Middle American genus. As defined by Stuart (1950) the Autochthonous Middle American fauna originated from "hanging relicts" left in Central America by the ancestral fauna that moved into South America and differentiated there at a time when South America was isolated from North and Middle America. The genus *Smilisca,* as we define it, consists of six species, all of which occur in Central America. One species ranges northward to southern Texas, and one extends southward on the Pacific lowlands of South America to Ecuador. We consider the genus *Smilisca* to be composed of rather generalized hylids. Consequently, an understanding of the systematics and zoogeography of the genus can be expected to be of aid in studying more specialized members of the family.

Acknowledgments

Examination of many of the specimens used in our study was possible only because of the cooperation of the curators of many systematic collections. For lending specimens or providing working space in their respective institutions we are grateful to Doris M. Cochran, Alice G. C. Grandison, Jean Guibe, Robert F. Inger, Günther Peters, Gerald Raun, William J. Riemer, Jay M. Savage, Hobart M. Smith, Wilmer W. Tanner, Charles F. Walker, Ernest E. Williams, and Richard G. Zweifel.

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We especially thank Charles J. Cole for contributing the information on the chromosomes, and Robert R. Patterson for preparing osteological specimens. We thank M. J. Fouquette, Jr., who read the section on breeding calls and offered constructive criticism.

Permits for collecting were generously provided by Ing. Rodolfo Hernandez Corzo in México, Sr. Jorge A. Ibarra in Guatemala, and Ing. Milton Lopez in Costa Rica. This report was made possible by support from the National Science Foundation (Grants G-9827 and GB-1441) and the cooperation of the Museum of Natural History at the University of Kansas. Some of the field studies were carried out in Panamá under the auspices of a grant from the National Institutes of Health (NIH GM-12020) in cooperation with the Gorgas Memorial Laboratory in Panamá.

Materials and Methods

In our study we examined 4151 preserved frogs, 93 skeletal preparations, 88 lots of tadpoles and young, and six lots of eggs. We have collected specimens in the field of all of the species. Observations on behavior and life history were begun by the senior author in México in 1956 and completed by us in Central America in 1964 and 1965.

Osteological data were obtained from dried skeletons and cleared and stained specimens of all species, plus serial sections of the skull of *Smilisca baudini*. Developmental stages to which tadpoles are assigned are in accordance with the table of development published by Gosner (1960). Breeding calls were recorded in the field on tape using Magnemite and Uher portable tape recorders. Audiospectrographs were made by means of a Vibralyzer (Kay Electric Company). External morphological features were measured in the manner described by Duellman (1956). In the accounts of the species we have attempted to give a complete synonymy. At the end of each species account the localities from which specimens were examined are listed alphabetically within each state, province, or department, which in turn are listed alphabetically within each country. The countries are arranged from north to south. Abbreviations for museum specimens are listed below:

AMNH—American Museum of Natural History
BMNH—British Museum (Natural History)
BYU—Brigham Young University
CNHM—Chicago Natural History Museum
KU—University of Kansas Museum of Natural History
MCZ—Museum of Comparative Zoology
MNHN—Museu National d'Histoire Naturelle, Paris
UF—University of Florida Collections
UIMNH—University of Illinois Museum of Natural History
UMMZ—University of Michigan Museum of Zoology
USC—University of Southern California
USNM—United States National Museum
TNHC—Texas Natural History Collection, University of Texas
ZMB—Zoologisches Museum Berlin

Genus Smilisca Cope, 1865

Smilisca Cope, Proc. Acad. Nat. Sci. Philadelphia, 17:194, Oct., 1865 [Type species *Smilisca daulinia* Cope, 1865 = *Hyla baudini* Duméril and Bibron, 1841]. Smith and Taylor, Bull. U. S. Natl. Mus., 194:75, June 17, 1948. Starrett, Copeia, 4:300, December 30, 1960. Goin, Ann. Carnegie Museum, 36:15, July 14, 1961.

Definition.—Medium to large tree frogs having: (1) broad, well ossified skull (consisting of a minimum amount of cartilage and/or secondarily ossified cartilage), (2) no dermal co-ossification, (3) quadratojugal and internasal septum present, (4) large ethmoid, (5) *M. depressor mandibulae* consisting of two parts, one arising from dorsal fascia and other from posterior arm of squamosal, (6) divided *M. adductor mandibulae,* (7) paired subgular vocal sacs in males, (8) no dermal appendages, (9) pupil horizontally elliptical (10) small amounts of amines and other active substances in skin, (11) chromosome number of N = 12 and 2N = 24, (12) breeding call consisting of poorly modulated, explosive notes, and (13) ⅔ tooth-rows in tadpoles.

Composition of genus.—As defined here the genus *Smilisca* contains six recognizable species. An alphabetical list of the specific and subspecific names

that we consider to be applicable to species of *Smilisca* recognized herein is given below.

Names proposed	Valid names
Hyla baudini Duméril and Bibron, 1841	= *S. baudini*
Hyla baudini dolomedes Barbour, 1923	= *S. phaeota*
Hyla beltrani Taylor, 1942	= *S. baudini*
Hyla gabbi Cope, 1876	= *S. sordida*
Hyla labialis Peters, 1863	= *S. phaeota*
Hyla manisorum Taylor, 1954	= *S. baudini*
Hyla muricolor Cope, 1862	= *S. baudini*
Hyla nigripes Cope, 1876	= *S. sordida*
Hyla pansosana Brocchi, 1877	= *S. baudini*
Hyla phaeota Cope, 1862	= *S. phaeota*
Hyla phaeota cyanosticta Smith, 1953	= *S. cyanosticta*
Hyla puma Cope, 1885	= *S. puma*
Hyla salvini Boulenger, 1882	= *S. sordida*
Hyla sordida Peters, 1863	= *S. sordida*
Hyla vanvlietii Baird, 1854	= *S. baudini*
Hyla vociferans Baird, 1859	= *S. baudini*
Hyla wellmanorum Taylor, 1952	= *S. puma*

Distribution of genus.—Most of lowlands of México and Central America, in some places to elevations of nearly 2000 meters, southward from southern Sonora and Río Grande Embayment of Texas, including such continental islands as Isla Cozumel, México, and Isla Popa and Isla Cebaco, Panamá, to northern South America, where known from Caribbean coastal regions and valleys of Río Cauca and Río Magdalena in Colombia, and Pacific slopes of Colombia and northern Ecuador.

Key to Adults

1. Larger frogs (♂ to 76 mm., ♀ to 90 mm.) having broad flat heads and a dark brown or black postorbital mark encompassing tympanum.....2
   Smaller frogs (♂ to 45 mm., ♀ to 64 mm.) having narrower heads and lacking a dark brown or black postorbital mark encompassing tympanum....4
2. Lips barred; flanks cream-colored with bold brown or black mottling in groin; posterior surfaces of thighs brown with cream-colored flecks, *S. baudini*, p. 289
   Lips not barred; narrow white labial stripe present; flanks not cream-colored with bold brown or black mottling in groin; posterior surfaces of thighs variable.....3
3. Flanks and anterior and posterior surfaces of thighs dark brown with large pale blue spots on flanks and small blue spots on thighs, *S. cyanosticta*, p. 303
   Flanks cream-colored with fine black venation; posterior surfaces of thighs pale brown with or without darker flecks or small cream-colored spots.....*S. phaeota*, p. 308
4. Fingers having only vestige of web; diameter of tympanum two-thirds that of eye; dorsum pale yellowish tan with pair of broad dark brown stripes.....*S. puma*, p. 314
   Fingers about one-half webbed; diameter of tympanum about one-half that of eye; dorsum variously marked with spots or blotches.....5
5. Snout short, truncate; vocal sacs in breeding males dark gray or brown; blue spots on flanks and posterior surfaces of thighs.....*S. sila*, p. 318
   Snout long, sloping, rounded; vocal sacs in breeding males white; cream-colored or pale blue flecks on flanks and posterior surfaces of thighs, *S. sordida*, p. 323

Key to Tadpoles

1. Pond tadpoles; tail about half again as long as body; mouth anteroventral.....2
   Stream tadpoles; tail about twice as long as body; mouth ventral.....5
2. Labial papillae in two rows.....3
   Labial papillae in one row.....4
3. First upper tooth row strongly arched medially; third lower tooth row much shorter than other rows; dorsal fin deepest at about two-thirds length of tail; tail cream-colored with dense gray reticulations, *S. puma*, p. 314
   First upper tooth row not arched medially; third lower tooth row nearly as long as others; dorsal fin deepest at about one-third length of tail; tail tan with brown flecks and blotches.....*S. baudini*, p. 289
4. Dorsal fin extending onto body.....*S. phaeota*, p. 308
   Dorsal fin not extending onto body.....*S. cyanosticta*, p. 303
5. Mouth completely bordered by two rows of papillae; inner margin of upper beak not forming continuous arch with lateral processes; red or reddish brown markings on tail.....*S. sordida*, p. 323
   Median part of upper lip bare; rest of mouth bordered by one row of papillae; inner margin of upper beak forming continuous arch with lateral processes; dark brown markings on tail.....*S. sila*, p. 318

ACCOUNTS OF SPECIES

Smilisca baudini (Duméril and Bibron)

Hyla baudini Duméril and Bibron, Erpétologie général, 8:564, 1841 [Holotype.—MNHN 4798 from "Mexico;" Baudin collector]. Günther, Catalogue Batrachia Salientia in British Museum, p. 105, 1858. Brocchi, Mission scientifique au Mexique . . ., pt. 3, sec. 2, Études sur les batrachiens, p. 29, 1881. Boulenger, Catalogue Batrachia Salientia in British Museum, p. 371, Feb. 1, 1882. Werner, Abhand. Zool-Bot. Gesell. Wien., 46:8, Sept. 30, 1896. Günther, Biologia Centrali-Americana: Reptilia and Batrachia, p. 270, Sept. 1901. Werner, Abhand. Konigl. Akad. Wiss. Munchen, 22:351, 1903. Cole and Barbour, Bull. Mus. Comp. Zool., 50(5):154, Nov. 1906. Gadow, Through southern México, p. 76, 1908. Ruthven, Zool. Jahr. 32(4):310, 1912. Decker, Zoologica, 2:12, Oct., 1915. Stejneger and Barbour, A checklist of North American amphibians and reptiles, p. 32, 1917. Noble, Bull. Amer. Mus. Nat. Hist., 38(10):341, June 20, 1918. Nieden, Das Tierreich, Amphibia, Anura I, p. 243, June, 1923. Gadow, Jorullo, p. 54, 1930. Dunn and Emlen, Proc. Acad. Nat. Sci. Philadelphia, 84:24, March 22, 1932. Kellogg, Bull. U. S. Natl. Mus., 160:160, March 31, 1932. Martin, Aquarien Berlin, p. 92, 1933. Stuart, Occas. Papers Mus. Zool., Univ. Michigan, 292:7, June 29, 1934; Misc. Publ. Mus. Zool. Univ. Michigan, 29:38, Oct. 1, 1935. Gaige, Carnegie Inst. Washington, 457:293, Feb. 5, 1936. Gaige, Hartweg, and Stuart, Occas. Papers Mus. Zool. Univ. Michigan, 360:5, Nov. 20, 1937. Smith, Occas. Papers Mus. Zool. Univ. Michigan, 388:2, 12, Oct. 31, 1938; Ann. Carnegie Mus., 27:312, March 14, 1939. Taylor, Copeia, 2:98, July 12, 1939. Hartweg and Oliver, Misc. Publ. Mus. Zool. Univ. Michigan, 47:12, July 13, 1940. Schmidt and Stuart, Zool. Ser. Field Mus. Nat. Hist., 24(21):238, August 30, 1941. Schmidt, Zool. Ser. Field Mus. Nat. Hist., 22(8):486, Dec. 30, 1941. Wright and Wright, Handbook of frogs and toads, Ed. 2, p. 134, 1942. Stuart, Occas. Papers Mus. Zool. Univ. Michigan, 471:15, May 17, 1943. Bogert and Oliver, Bull. Amer. Mus. Nat. Hist., 83(6):343, March 30, 1945. Taylor and Smith, Proc. U. S. Natl. Mus., 95(3185):590, June 30, 1945. Smith, Ward's Nat. Sci. Bull., 1, p. 3, Sept., 1945. Schmidt and Shannon, Fieldiana, Zool. Chicago Nat. Hist. Mus., 31(9):67, Feb.

20, 1947. Stuart, Misc. Publ. Mus. Zool. Univ. Michigan, 69:26, June 12, 1948. Wright and Wright, Handbook of frogs and toads, Ed. 3, p. 298, 1949. Stuart, Contr. Lab. Vert. Biol. Univ. Michigan, 45:22, May, 1950. Mertens, Senckenbergiana, 33:170, June 15, 1952; Abhand. Senckenb. Naturf. Gesell., 487:28, Dec. 1, 1952. Schmidt, A checklist of North American amphibians and reptiles, Ed. 6, p. 69, 1953. Stuart Contr. Lab. Vert. Biol. Univ. Michigan, 68:46, Nov. 1954. Zweifel and Norris, Amer. Midl. Nat., 54(1):232, July 1955. Martin, Amer. Nat., 89:356, Dec. 1955. Duellman, Copeia, 1:49, Feb. 21, 1958. Goin, Herpetologica, 14:119, July 23, 1958. Turner, Herpetologica, 14:192, Dec. 1, 1958. Conant, A field guide to reptiles and amphibians, p. 284, 1958. Duellman, Univ. Kansas Publ., Mus. Nat. Hist., 13(2):59, Aug. 16, 1960; Univ. Kansas Publ., Mus. Nat. Hist., 15(1): 46, Dec. 20, 1961. Porter, Herpetologica, 18:165, Oct. 17, 1962.

Hyla vanvlietii Baird, Proc. Acad. Nat. Sci. Philadelphia, 7:61, April 27, 1854 [Holotype.—USNM 3256 from Brownsville, Cameron County, Texas; S. Van Vliet collector]. Baird, United States and Mexican boundary survey, 2:29, 1859. Smith and Taylor, Univ. Kansas Sci. Bull., 33: 361, March 20, 1950. Cochran, Bull. U. S. Natl. Mus., 220:60, 1961.

Hyla vociferans Baird, United States and Mexican boundary survey, 2:35 1859 [*nomen nudum*]. Díaz de León, Indice de los batracios que se encuentran en la República Mexicana, p. 20, June 1904.

Hyla muricolor Cope, Proc. Acad. Nat. Sci. Philadelphia, 14(9):359, 1862 [Holotype.—USNM 25097 from Mirador, Veracruz, México; Charles Sartorius collector]. Smith and Taylor, Univ. Kansas Sci. Bull., 33:349, March 20, 1950. Cochran, Bull. U. S. Natl. Mus., 220:56, 1961.

Smilisca daulinia Cope, Proc. Acad. Nat. Sci. Philadelphia, 17:194, Oct. 1865 [Holotype.—"skeleton in private anatomical museum of Hyrtl, Professor of Anatomy in the University of Vienna"]. Smith and Taylor, Univ. Kansas Sci. Bull., 33:347, March 20, 1950.

Smilisca daudinii [lapsus for *baudini*], Cope, Proc. Acad. Nat. Sci. Philadelphia, 23, pt. 2:205, 1871.

Smilisca baudini, Cope, Bull. U. S. Nat. Mus., 1:31, 1875; Jour. Acad. Nat. Sci. Philadelphia, 8, pt. 2:107, 1876; Proc. Amer. Philos. Soc., 18:267, August 11, 1879. Yarrow, Bull. U. S. Nat. Mus., 24:176, July 1, 1882. Cope, Bull. U. S. Nat. Mus., 32:13, 1887; Bull. U. S. Nat. Mus., 34:379, April 9, 1889. Dickerson, The frog book, p. 151, July, 1906. Smith and Taylor, Univ. Kansas Sci. Bull., 33:442, March 20, 1950; Taylor, U. Kan. Sc. Bull., 34:802, Feb. 15, 1952; Univ. Kansas Sci. Bull., 35:794, July 1, 1952. Brattstrom, Herpetologica, 8(3):59, Nov. 1, 1952. Taylor, U. Kan. Sci. Bull., 35:1592, Sept. 10, 1953. Peters, Occas. Papers Mus. Zool. Univ. Michigan, 554:7, June 23, 1954. Duellman, Occas. Papers Mus. Zool. Univ. Michigan, 560:8, Oct. 22, 1954. Chrapliwy and Fugler, Herpetologica, 11:122, July 15, 1955. Smith and Van Gelder, Herpetologica, 11:145, July 15, 1955. Lewis and Johnson, Herpetologica, 11: 178, Nov. 30, 1955. Martin, Misc. Publ. Mus. Zool. Univ. Michigan, 101: 53, April 15, 1958. Stuart, Contr. Lab. Vert. Biol. Univ. Michigan, 75:17, June, 1958. Minton and Smith, Herpetologica, 17:74, July 11, 1961. Nelson and Hoyt, Herpetologica, 17:216, Oct. 9, 1961. Holman, Copeia, 2:256, July 20, 1962. Stuart, Misc. Publ. Mus. Zool. Univ. Michigan, 122:41, April 2, 1963. Maslin, Herpetologica, 19:124, July 3, 1963. Holman and Birkenholz, Herpetologica, 19:144, July 3, 1963. Duellman, Univ. Kansas Publ. Mus. Nat. Hist., 15(5):228, Oct. 4, 1963. Zweifel, Copeia, 1:206, March 26, 1964. Duellman and Klaas, Copeia, 2:313, June 30, 1964. Davis and Dixon, Herpetologica, 20:225, January 25, 1965. Neill, Bull. Florida State Mus., 9:89, April 9, 1965.

Hyla pansosana Brocchi, Bull. Soc. Philom., ser. 7, 1:125, 1877 [Holotype. —MNHN 6313 from Panzós, Alta Verapaz, Guatemala; M. Bocourt collector]; Mission scientifique au Mexique . . ., pt. 3, sec. 2, Études sur les batrachiens, p. 34, 1881.

Hyla baudini baudini, Stejneger and Barbour, A checklist of North American amphibians and reptiles, Ed. 3, p. 34, 1933. Wright and Wright, Handbook of frogs and toads, p. 110, 1933. Stejneger and Barbour, A checklist of North American amphibians and reptiles, Ed. 4, p. 39, 1939; A checklist of North American amphibians and reptiles, Ed. 5, p. 49, 1943. Smith and Laufe, Trans. Kansas Acad. Sci., 48(3):328, Dec. 19, 1945. Peters, Nat. Hist. Misc., 143:7, March 28, 1955.

Hyla beltrani Taylor, Univ. Kansas Sci. Bull. 28(14):306, Nov. 15, 1942 [Holotype.—UIMNH 25046 (formerly EHT-HMS 29563) from Tapachula, Chiapas, México; A. Magaña collector]. Smith and Taylor, Bull. U. S. Natl. Mus. 194:87, June 17, 1948; Univ. Kansas Sci. Bull., 33:326, March 20, 1950. Smith, Illinois Biol. Mono., 32:23, May, 1964.

Smilisca baudini baudini, Smith, Jour. Washington Acad. Sci., 37(11):408, Nov. 15, 1947. Smith and Taylor, Bull. U. S. Natl. Mus., 194:75, June 17, 1948; Univ. Kansas Sci. Bull., 33:347, March 20, 1950. Brown, Baylor Univ. Studies, p. 68, 1950. Smith, Smith, and Werler, Texas Jour. Sci., 4(2):254, June 30, 1952. Smith and Smith, Anales Inst. Biol., 22(2):561, Aug. 7, 1952. Smith and Darling, Herpetologica, 8(3):82, Nov. 1, 1952. Davis and Smith, Herpetologica, 8(4):148, Jan. 30, 1953. Neill and Allen, Publ. Res. Div. Ross Allen's Reptile Inst., 2(1):26, Nov. 10, 1959. Maslin, Univ. Colorado Studies, Biol. Series, 9:4, Feb. 1963. Holman, Herpetologica, 20:48, April 17, 1964.

Hyla manisorum Taylor, Univ. Kansas Sci. Bull., 36:630, June 1, 1954 [Holotype.—KU 34927 from Batán, Limón Province, Costa Rica; Edward H. Taylor collector]. Duellman and Berg, Univ. Kansas Publ. Mus. Nat. Hist., 15(4):193, Oct. 26, 1962.

Diagnosis.—Size large (♂ 76 mm., ♀ 90 mm.); skull noticeably wider than long, having small frontoparietal fontanelle (roofed with bone in large individuals); postorbital processes long, pointed, curving along posterior border of orbit; squamosal large, contacting maxillary; tarsal fold strong, full length of tarsus; inner metatarsal tubercle large, high, elliptical; hind limbs relatively short, tibia length less than 55 per cent snout-vent length; lips strongly barred with brown and creamy tan; flanks pale cream with bold brown or black reticulations in groin; posterior surfaces of thighs brown with cream-colored flecks; dorsal surfaces of limbs marked with dark brown transverse bands. (Foregoing combination of characters distinguishing S. *baudini* from any other species in genus.)

Description and Variation.—Considerable variation in size, and in certain proportions and structural characters was observed; variation in some characters seems to show geographic trends, whereas variation in other characters apparently is random. Noticeable variation is evident in coloration, but this will be discussed later.

In order to analyze geographic variation in size and proportions, ten adult males from each of 14 samples from various localities throughout the range of the species were measured. Snout-vent length, length of the tibia in relation to snout-vent length, and relative size of the tympanum to the eye are the only measurements and proportions that vary noticeably (Table 1). The largest specimens are from southern Sinaloa; individuals from the Atlantic lowlands of Alta Verapaz in Guatemala, Honduras, and Costa Rica are somewhat smaller, and most specimens from the Pacific lowlands of Central America are slightly smaller than those from the Atlantic lowlands. The smallest males are from the Atlantic lowlands of México, including Tamaulipas, Veracruz, the Yucatan Peninsula, and British Honduras.

TABLE 1.—GEOGRAPHIC VARIATION IN SIZE AND PROPORTIONS IN MALES OF SMILISCA BAUDINI. (MEANS IN PARENTHESES BELOW OBSERVED RANGES; DATA BASED OF 10 SPECIMENS FROM EACH LOCALITY.)

LOCALITY	Snout-vent length	Tibia length/ snout-vent	Tympanum/ eye
Southern Sinaloa	62.3–75.9 (68.6)	43.2–46.7 (44.9)	84.2–94.4 (87.8)
Ocotito, Guerrero	55.6–64.0 (58.7)	46.1–51.2 (47.8)	66.7–82.8 (74.6)
Pochutla, Oaxaca	56.1–65.1 (60.2)	44.7–49.4 (47.5)	73.0–84.2 (77.4)
San Salvador, El Salvador	57.0–68.0 (62.1)	42.1–46.1 (44.9)	74.6–83.3 (77.6)
Managua, Nicaragua	52.9–63.6 (57.3)	45.6–49.4 (47.5)	73.7–89.7 (79.4)
Esparta, Costa Rica	57.6–66.0 (61.3)	44.6–49.3 (47.3)	65.5–83.6 (75.2)
Ciudad Victoria, Tamaulipas	50.6–56.9 (53.7)	44.5–48.7 (46.6)	67.2–84.3 (73.9)
Córdoba, Veracruz	53.8–63.4 (57.5)	43.9–48.4 (45.6)	66.1–75.9 (70.0)
Isla del Carmen, Campeche	47.3–56.6 (50.9)	44.7–48.9 (47.6)	61.5–72.6 (65.7)
Chichén-Itzá, Yucatán	49.6–57.1 (53.8)	45.2–53.4 (49.5)	62.7–80.7 (72.6)
British Honduras	49.0–59.6 (54.9)	47.5–50.7 (49.1)	67.9–76.8 (72.2)
Chinajá, Guatemala	56.8–67.6 (63.2)	47.0–51.0 (49.5)	70.0–82.8 (73.6)
Atlantidad, Honduras	52.5–65.1 (57.6)	49.8–53.6 (51.5)	56.1–76.5 (67.0)
Limón, Costa Rica	57.7–71.3 (62.4)	50.4–52.3 (51.2)	63.9–73.0 (68.5)

The ratio of the tibia to the snout-vent length varies from 42.1 to 53.6 in the 14 samples analyzed. The average ratio in samples from the Pacific lowlands varies from 44.9 in Sinaloa and El Salvador to 47.8 in Guerrero; on the Gulf lowlands of México the average ratio varies from 45.6 in Veracruz to 47.6 on Isla del Carmen, Campeche. Specimens from the Yucatan Peninsula and the Caribbean lowlands have relatively longer legs; the variation in average ratios ranges from 49.1 in British Honduras to 51.2 in Costa Rica and 51.5 in Honduras.

Specimens from southern Sinaloa are outstanding in the large size of the

tympanum; the tympanum/eye ratio varies from 84.2 to 94.4 (average 87.8). In most other samples the variation in average ratios ranges from 72.2 to 79.3, but specimens from Veracruz have an average ratio of 70.0; Campeche, 65.7; Honduras, 67.0; and Limón, Costa Rica, 68.5.

No noticeable geographic trends in size and proportions are evident. Specimens from southern Sinaloa are extreme in their large size, relatively short tibia, and large tympani, but in size and relative length of the tibia the Sinaloan frogs are approached by specimens from such far-removed localities as San Salvador, El Salvador, and Chinajá, Guatemala. Frogs from the Caribbean lowlands of Honduras and Costa Rica are relatively large and have relatively long tibiae and small tympani.

The inner metatarsal tubercle is large and high and its shape varies. The tubercle is most pronounced in specimens from northwestern México, Tamaulipas, and the Pacific lowlands of Central America. Possibly the large tubercle is associated with drier habitats, where perhaps the frogs use the tubercles for digging.

The ground color of *Smilisca baudini* is pale green to brown dorsally and white to creamy yellow ventrally. The dorsum is variously marked with dark brown or dark olive-green spots or blotches (Pl. 6A). In most specimens a dark interorbital bar extends across the head to the lateral edges of the eyelid; usually this bar is connected medially to a large dorsal blotch. There is no tendency for the markings on the dorsum to form transverse bands or longitudinal bars. In specimens from the southern part of the range the dorsal dark markings are often fragmented into small spots, especially posteriorly. The limbs are marked by dark transverse bands, usually three on the forearm, three on the thigh, and three or four on the shank. Transverse bands also are present on the tarsi and proximal segments of the fingers and toes. The webbing on the hands and feet is pale grayish brown. The loreal region and upper lip are pale green or tan; the lip usually is boldly marked with broad vertical dark brown bars, especially evident is the bar beneath the eye. A dark brown or black mark extends from the tympanum to a point above the insertion of the forearm; in some specimens this black mark is narrow or indistinct, but in most individuals it is quite evident. The flanks are pale gray to creamy white with brown or black mottling, which sometimes forms reticulations enclosing white spots. The anterior surfaces of the thighs usually are creamy white with brown mottling, whereas the posterior surfaces of the thighs usually are brown with small cream colored flecks. A distinct creamy-white anal stripe usually is present. Usually, there are no white stripes on the outer edges of the tarsi and forearms. In breeding males the throat is gray.

Most variation in coloration does not seem to be correlated with geography. The lips are strongly barred in specimens from throughout the range of the species, except that in some specimens from southern Nicaragua and Costa Rica the lips are pale and in some specimens the vertical bars are indistinct. Six specimens from 7.3 kilometers southwest of Matatán, Sinaloa, are distinctively marked. The dorsum is uniformly grayish green with the only dorsal marks being on the tarsi; canthal and post-tympanic dark marks absent. A broad white labial stripe is present and interrupted by a single vertical dark mark below the eye. A white stripe is present on the outer edge of the foot. The flanks and posterior surfaces of the thighs are creamy white, boldly marked with black. Two specimens from Alta Verapaz, Guatemala (CNHM 21006

from Cobán and UMMZ 90908 from Finca Canihor), are distinctive in having many narrow transverse bands on the limbs and fine reticulations on the flanks. Two specimens from Limón Province, Costa Rica (KU 34927 from Batán and 36789 from Suretka), lack a dorsal pattern; instead these specimens are nearly uniform brown above and have only a few small dark brown spots on the back and lack transverse bands on the limbs. The post-tympanic dark marks and dark mottling on the flanks are absent. Specimens lacking the usual dorsal markings are known from scattered localities on the Caribbean lowlands from Guatemala to Costa Rica.

The coloration in life is highly variable; much of the apparent variation is due to metachrosis, for individuals of *Smilisca baudini* are capable of undergoing drastic and rapid change in coloration. When active at night the frogs usually are pale bright green with olive-green markings, olive-green with brown markings, or pale brown with dark brown markings. The dark markings on the back and dorsal surfaces of the limbs are narrowly outlined by black. The pale area below the eye and just posterior to the broad suborbital dark bar is creamy white, pale green, or ashy gray in life. The presence of this mark is an excellent character by which to identify juveniles of the species. The flanks are creamy yellow, or yellow with brown or black mottling. In most individuals the belly is white, but in specimens from southern El Petén and northern Alta Verapaz, Guatemala, the belly is yellow, especially posteriorly. The iris varies from golden bronze to dull bronze with black reticulations, somewhat darker ventrally.

Natural History.—Throughout most of its range *Smilisca baudini* occurs in subhumid habitats; consequently the activity is controlled by the seasonal nature of the rainfall and usually extends from May or June through September. Throughout México and Central America the species is known to call and breed in June, July, and August. Several records indicate that the breeding season in Central America is more lengthy. Gaige, Hartweg, and Stuart (1937:4) noted gravid females collected at El Recreo, Nicaragua, in August and September. Schmidt (1941:486) reported calling males in February in British Honduras. Stuart (1958:17) stated that tadpoles were found in mid-February, juveniles in February and March and half-grown individuals from mid-March to mid-May at Tikal, El Petén, Guatemala. Stuart (1961:74) reported juveniles from Tikal in July, and that individuals were active at night when there had been light rain in the dry season in February and March in El Petén, Guatemala. *Smilisca baudini* seeks day-time retreats in bromeliads, elephant-ear plants (*Xanthosoma*), and beneath bark or in holes in trees. By far the most utilized retreat in the dry season in parts of the range is beneath the outer sheaths of banana plants. Large numbers of these frogs were found in banana plants at Cuautlapan, Veracruz, in March, 1956, in March and December, 1959.

Large breeding congregations of this frog are often found at the time of the first heavy rains in the wet season. Gadow (1908:76) estimated 45,000 frogs at one breeding site in Veracruz. In the vicinity of Tehuantepec, Oaxaca, large numbers of individuals were found around rain pools and roadside ditches in July, 1956, and July, 1958; large concentrations were found near Chinajá, Guatemala, in June, 1960, and near Esparta, Costa Rica in July, 1961. Usually males call from the ground at the edge of the water or not infrequently sit in shallow water, but sometimes males call from bushes and low trees

around the water. Stuart (1935:38) recorded individuals calling and breeding throughout the day at La Libertad, Guatemala. *Smilisca baudini* usually is absent from breeding congregations of hylids; frequently *S. baudini* breeds alone in small temporary pools separated from large ponds where numerous other species are breeding. In Guerrero and Oaxaca, México, *S. baudini* breeds in the same ponds with *Rhinophrynus dorsalis, Bufo marmoreus, Engystomops pustulosus,* and *Diaglena reticulata,* and in the vicinity of Esparta, Costa Rica, *S. baudini* breeds in ponds with *Bufo coccifer, Hyla staufferi,* and *Phrynohyas venulosa.* In nearly all instances the breeding sites of *S. baudini* are shallow, temporary pools.

The breeding call of *Smilisca baudini* consists of a series of short explosive notes. Each note has a duration of 0.09 to 0.13 seconds; two to 15 notes make up a call group. Individual call groups are spaced from about 15 seconds to several minutes apart. The notes are moderately high-pitched and resemble "wonk-wonk-wonk." Little vibration is discernible in the notes, which have 140 to 195 pulses per second and a dominant frequency of 2400 to 2725 cycles per second (Pl. 10A).

The eggs are laid as a surface film on the water in temporary pools. The only membrane enclosing the individual eggs is the vitelline membrane. In ten eggs (KU 62154 from San Salvador, El Salvador) the average diameter of the embryos in first cleavage is 1.3 mm. and of the vitelline membranes, 1.5 mm. Hatchling tadpoles have body lengths of 2.6 to 2.7 mm. and total lengths of 5.1 to 5.4 mm. The body and caudal musculature is brown; the fins are densely flecked with brown. The gills are long and filamentous. Growth and development of tadpoles are summarized in Table 9.

A typical tadpole in stage 30 of development (KU 60018 from Chinajá, Alta Verapaz, Guatemala) has a body length of 8.7 mm., a tail length of 13.6 mm., and a total length of 22.3 mm.; body slightly wider than deep; snout rounded dorsally and laterally; eyes widely separated, directed dorsolaterally; nostril about midway between eye and tip of snout; mouth anteroventral; spiracle sinistral, located about midway on length of body and slightly below midline; anal tube dextral; caudal musculature slender, slightly curved upward distally; dorsal fin extending onto body, deepest at about one-third length of tail; depth of dorsal fin slightly more than that of ventral fin at midlength of tail; dorsal part of body dark brown; pale crescent-shaped mark on posterior part of body; ventral surfaces transparent with scattered brown pigment ventrolaterally, especially below eye; caudal musculature pale tan with a dark brown longitudinal streak on middle of anterior one-third of tail; dorsum of anterior one-third of tail dark brown; brown flecks and blotches on rest of caudal musculature, on all of dorsal fin, and on posterior two-thirds of ventral fin; iris bronze in life (Fig. 11). Mouth small; median third of upper lip bare; rest of mouth bordered by two rows of conical papillae; lateral fold present; tooth rows 2/3; two upper rows about equal in length; second row broadly interrupted medially, three lower rows complete, first and second equal in length, slightly shorter than upper rows; third lower row shortest; first upper row sharply curved anteriorly in midline; upper beak moderately deep, forming a board arch with slender lateral processes; lower beak more slender, broadly V-shaped; both beaks bearing blunt serrations (Fig. 15A).

In tadpoles having fully developed mouthparts the tooth-row formula of 2/3 is invariable, but the coloration is highly variable. The color and pattern

described above is about average. Some tadpoles are much darker, such as those from 11 kilometers north of Vista Hermosa, Oaxaca, (KU 87639-44), 3.5 kilometers east of Yokdzonot, Yucatán (KU 71720), and 4 kilometers west-southwest Puerto Juárez, Quintana Roo, México (KU 71721), whereas others, notably from 17 kilometers northeast of Juchatengo, Oaxaca, México (KU 87645), are much paler and lack the dark markings on the caudal musculature. The variation in intensity of pigmentation possibly can be correlated with environmental conditions, especially the amount of light. In general, tadpoles that were found in open, sunlit pools are pallid by comparison with those from shaded forest pools. These subjective comparisons were made with preserved specimens; detailed comparative data on living tadpoles are not available.

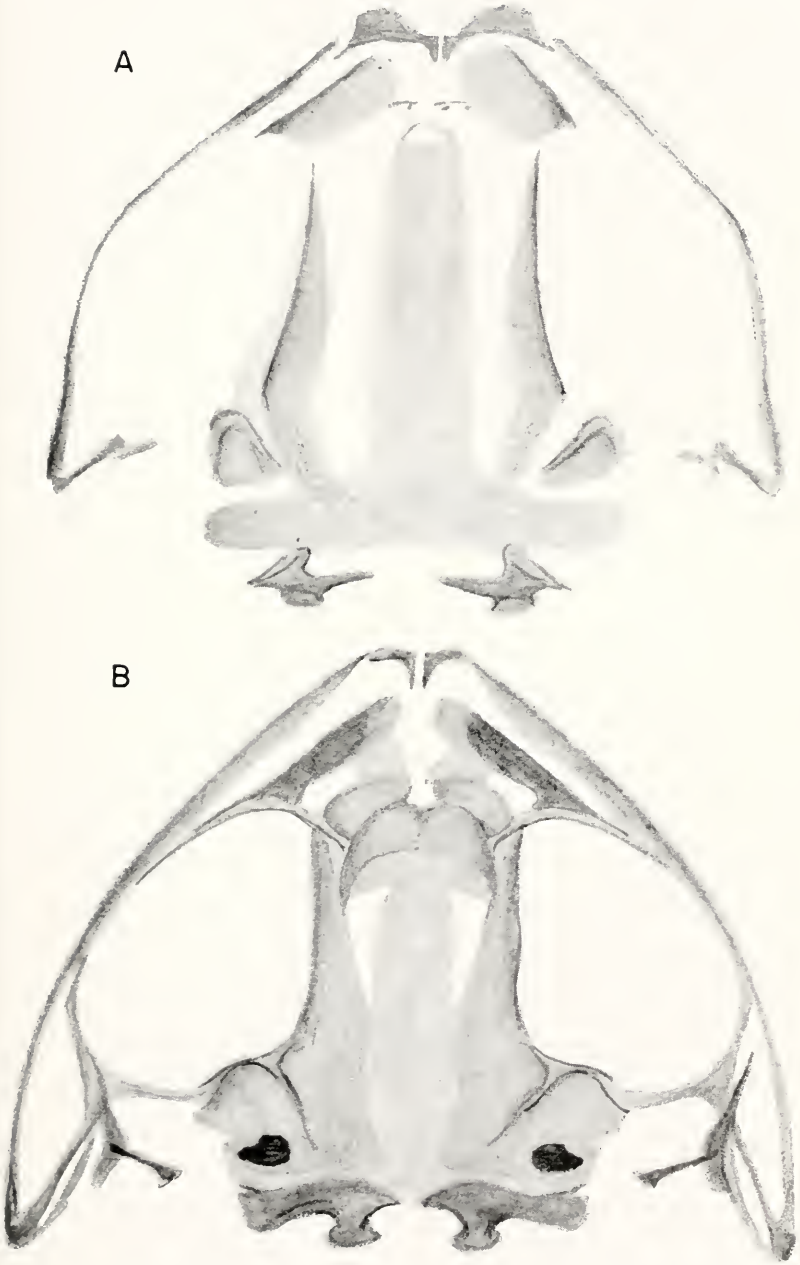
The relative length and depth of the tail are variable; in some individuals the greatest depth of the tail is about at mid-length of the tail, whereas in most specimens the tail is deepest at about one-third its length. The length of the tail relative to the total length is usually 58 to 64 per cent in tadpoles in stages 29 and 30 of development. In some individuals the tail is about 70 per cent of the total length. On the basis of the material examined, these variations in proportions do not show geographical trends. Probably the proportions are a reflection of crowding of the tadpoles in the pools where they are developing or possibly due to water currents or other environmental factors.

Stuart (1948:26) described and illustrated the tadpole of *Smilisca baudini* from Finca Chejel, Alta Verapaz, Guatemala. The description and figures agree with ours, except that the first lower tooth row does not have a sharp angle medially in Stuart's figure. He (1948:27) stated that color in tadpoles from different localities probably varies with soil color and turbidity of water. Maslin (1963:125) described and illustrated tadpoles of *S. baudini* from Pisté, Yucatán, México. These specimens are heavily pigmented like specimens that we have examined from the Yucatan Peninsula and from other places in the range of the species. Maslin stated that the anal tube is median in the specimens that he examined; we have not studied Maslin's specimens, but all tadpoles of *Smilisca* that we have examined have a dextral anal tube.

Newly metamorphosed young have snout-vent lengths of 12.0 to 15.5 mm. (average 13.4 in 23 specimens). The largest young are from La Libertad, El Petén, Guatemala; these have snout-vent lengths of 14.0 to 15.5 mm. (average 14.5 in five specimens). Young from 11 kilometers north of Vista Hermosa, Oaxaca, México, are the smallest and have snout-vent lengths of 12.0 to 12.5 mm. (average 12.3 in three specimens). Recently metamorphosed young usually are dull olive green above and white below; brown transverse bands are visible on the hind limbs. The labial markings characteristic of the adults are represented only by a creamy white suborbital spot, which is a good diagnostic mark for young of this species. In life the iris is pale gold.

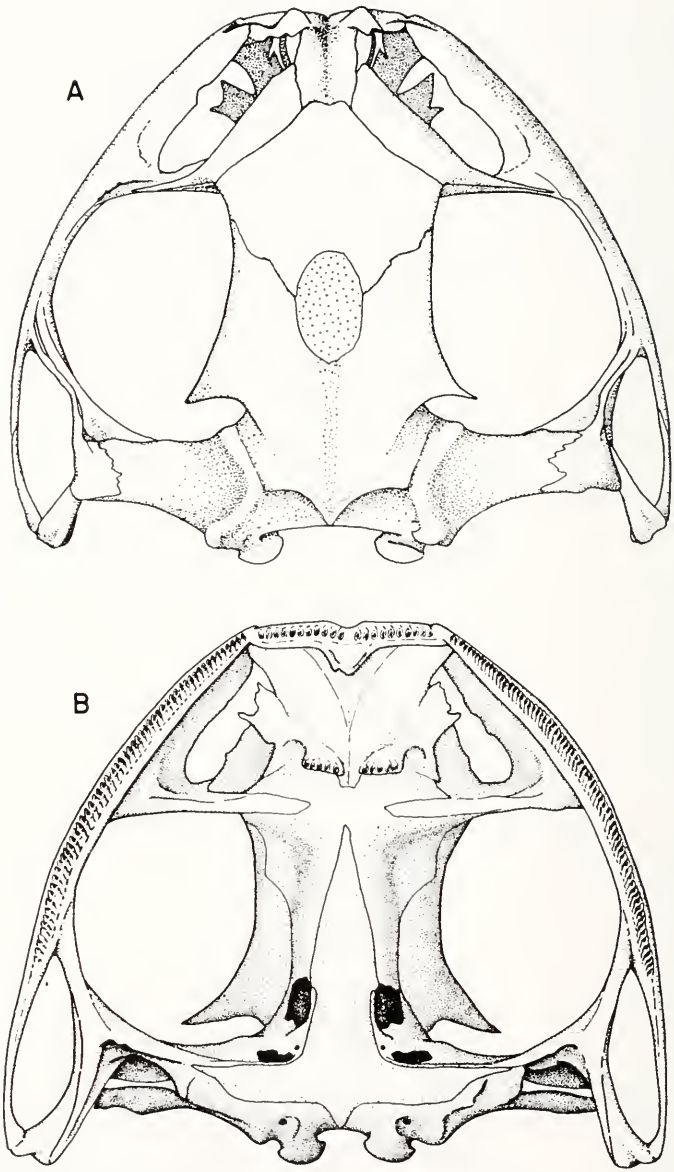
Remarks: The considerable variation in color and the extensive geographic distribution of *Smilisca baudini* have resulted in the proposal of eight specific names for the frogs that we consider to represent one species. Duméril and Bibron (1841:564) proposed the name *Hyla baudini* for a specimen (MNHN 4798) from México. Smith and Taylor (1950:347) restricted the type locality to Córdoba, Veracruz, México, an area where the species occurs in abundance. Baird (1854:61) named *Hyla vanvlieti* from Brownsville, Texas, and (1859:35) labelled the figures of *Hyla vanvlieti* [= *Hyla baudini*] on plate 38 as *Hyla vociferans*, a *nomen nudum*. Cope (1862:359) named *Hyla muricolor* from Mirador, Veracruz, México, and (1865:194) used the name *Smilisca daulinia*

PLATE 1



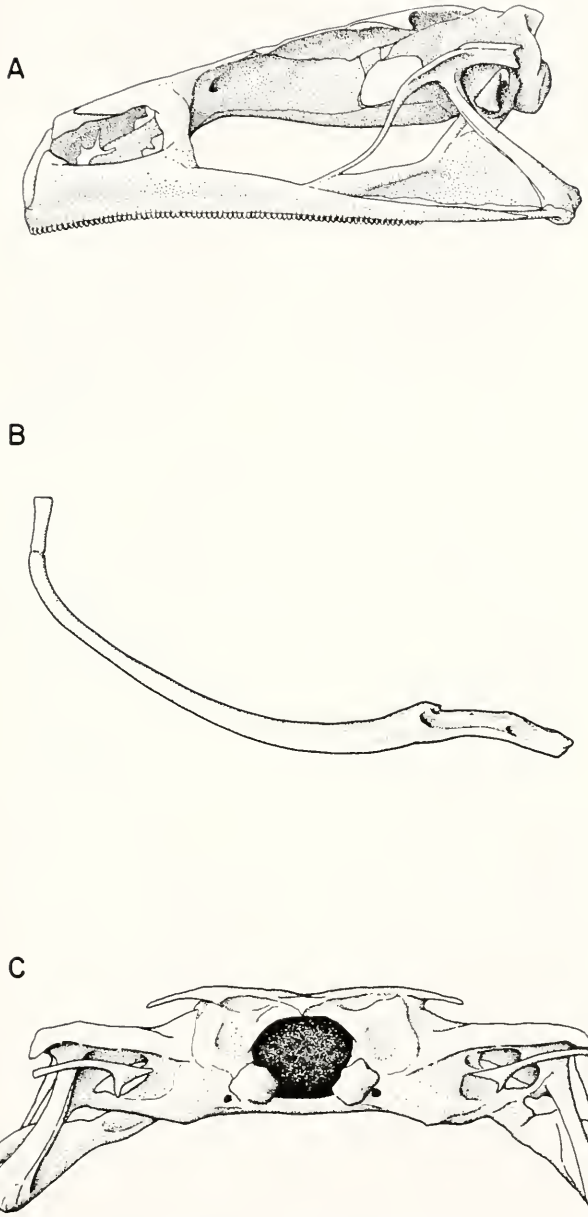
Dorsal views of skulls of young *Smilisca baudini:* (A) recently metamorphosed young (KU 60026), snout-vent length 12.6 mm. ×23; (B) young (KU 85438), snout-vent length 32.1 mm. ×9.

PLATE 2



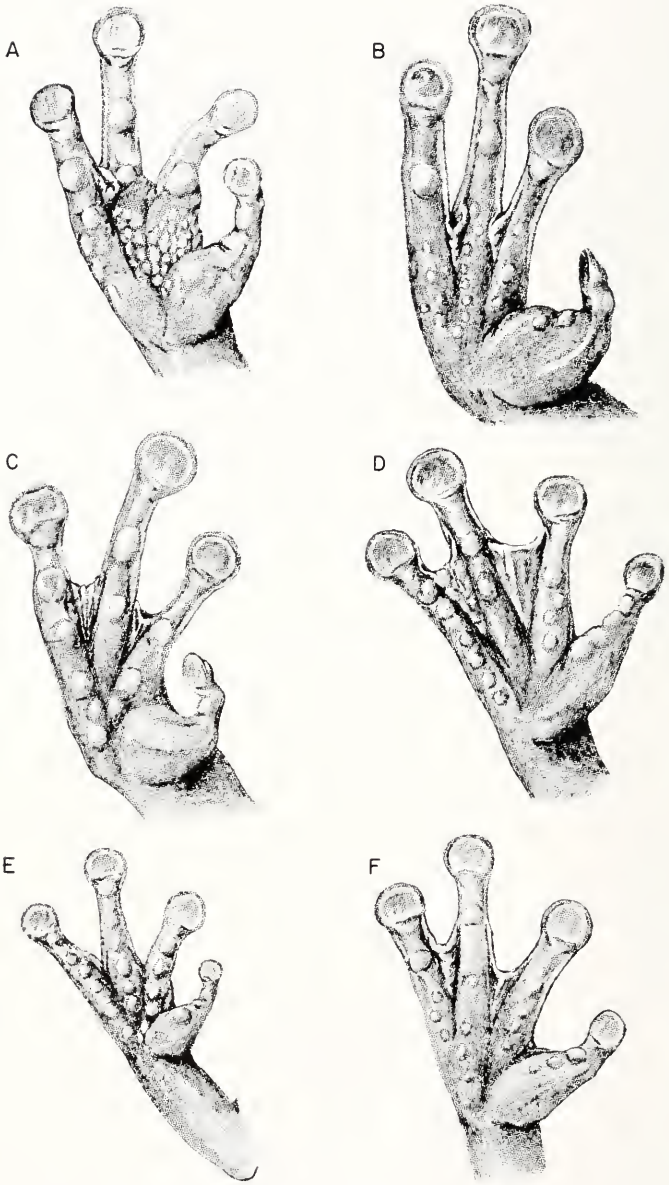
Skull of adult female *Smilisca baudini* (KU 68184): (A) Dorsal; (B) Ventral. ×4.5.

PLATE 3



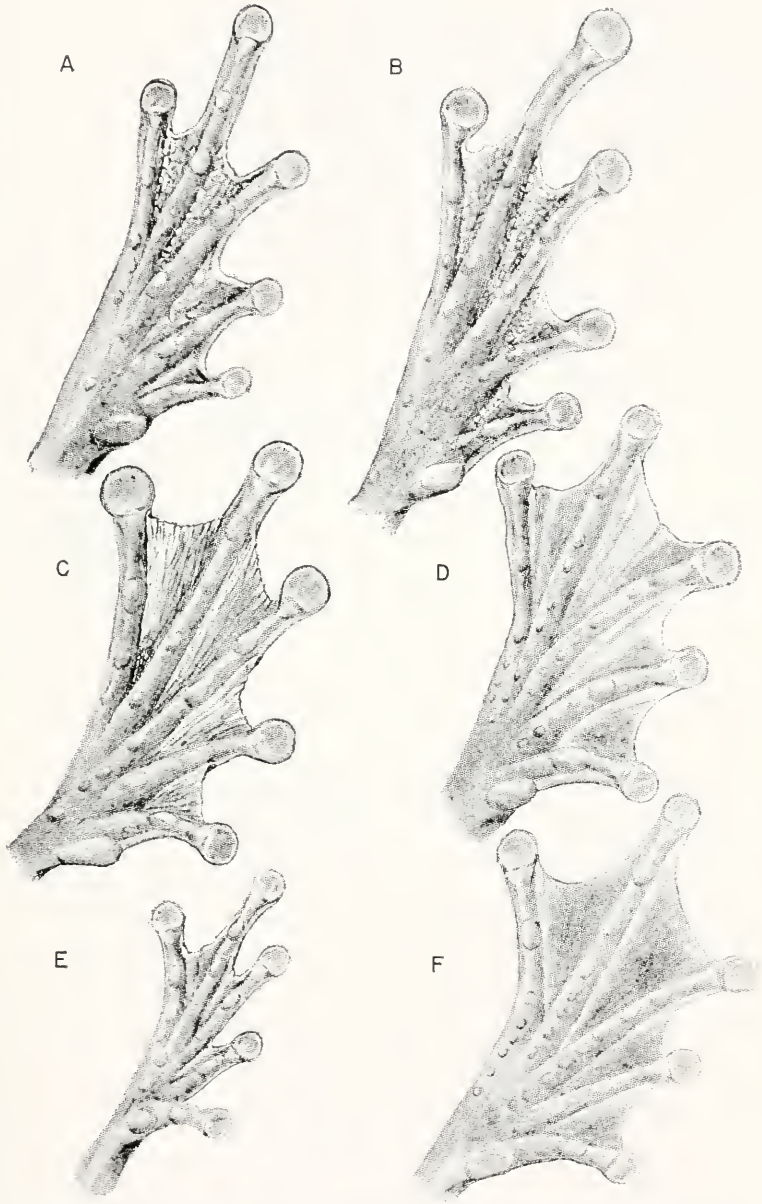
Skull of adult female *Smilisca baudini* (KU 68184): (A) Lateral; (B) Dorsal view of left mandible; (C) Posterior. ×4.5.

PLATE 4



Palmar views of right hands of *Smilisca:* (A) S. *baudini* (KU 87177); (B) S. *phaeota* (KU 64276); (C) S. *cyanosticta* (KU 87199); (D) S. *sordida* (KU 91761; (E) S. *puma* (KU 91716), and (F) S. *sila* (KU 77408). ×3.

PLATE 5

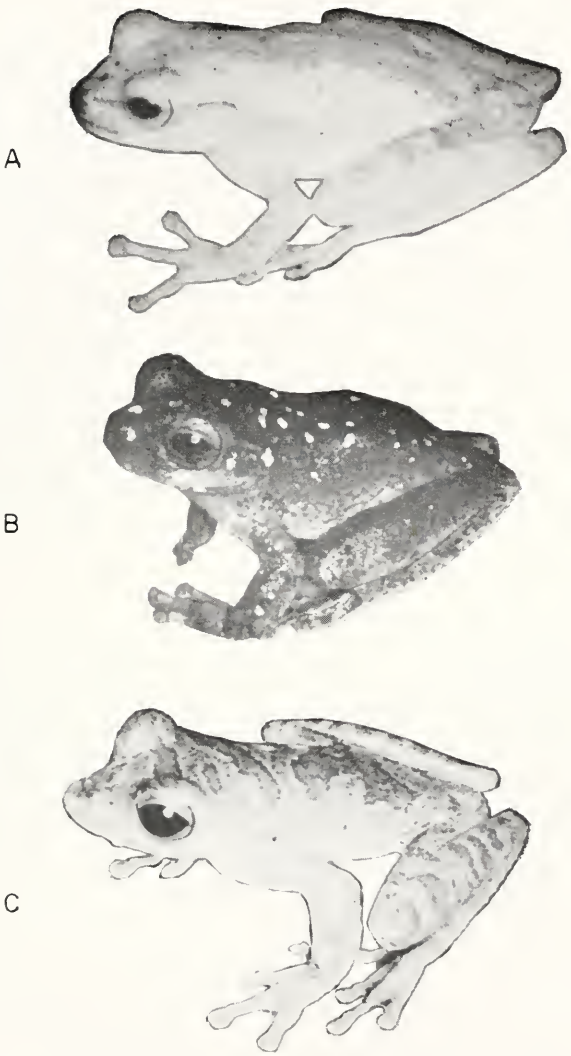


Ventral aspect of right feet of *Smilisca:* (A) *S. baudini* (KU 87177); (B) *S. phaeota* (KU 64276); (C) *S. cyanosticta* (KU 87199); (D) *S. sordida* (KU 91761); (E) *S. puma* (KU 91716), and (F) *S. sila* (KU 77408). ×3.

PLATE 6

Living *Smilisca:* (A) *S. baudini* (UMMZ 115179) from 1.7 km. W Xicotencatal, Tamaulipas, México; (B) *S. cyanosticta* (UMMZ 118163) from Volcán San Martín, Veracruz, México; (C) *S. phaeota* (KU 64282) from Barranca del Río Sarapiqui, Heredia Prov., Costa Rica. All approx. nat. size.

PLATE 7



Living *Smilisca:* (A) *S. puma* (KU 65307) from 5.9 km. W. Puerto Viejo, Heredia Prov., Costa Rica; (B) *S. sila* (KU 77407) from Finca Palosanto, 6 km. WNW El Volcán, Chiriquí, Panamá; (C) *S. sordida* (KU 64257) from 20 km. WSW San Isidro el General, San José Prov., Costa Rica. All approx. nat. size.

FIG. 1. Breeding site of *Smilisca baudini*, 4 km. WNW of Esparta, Puntarenas Prov., Costa Rica.

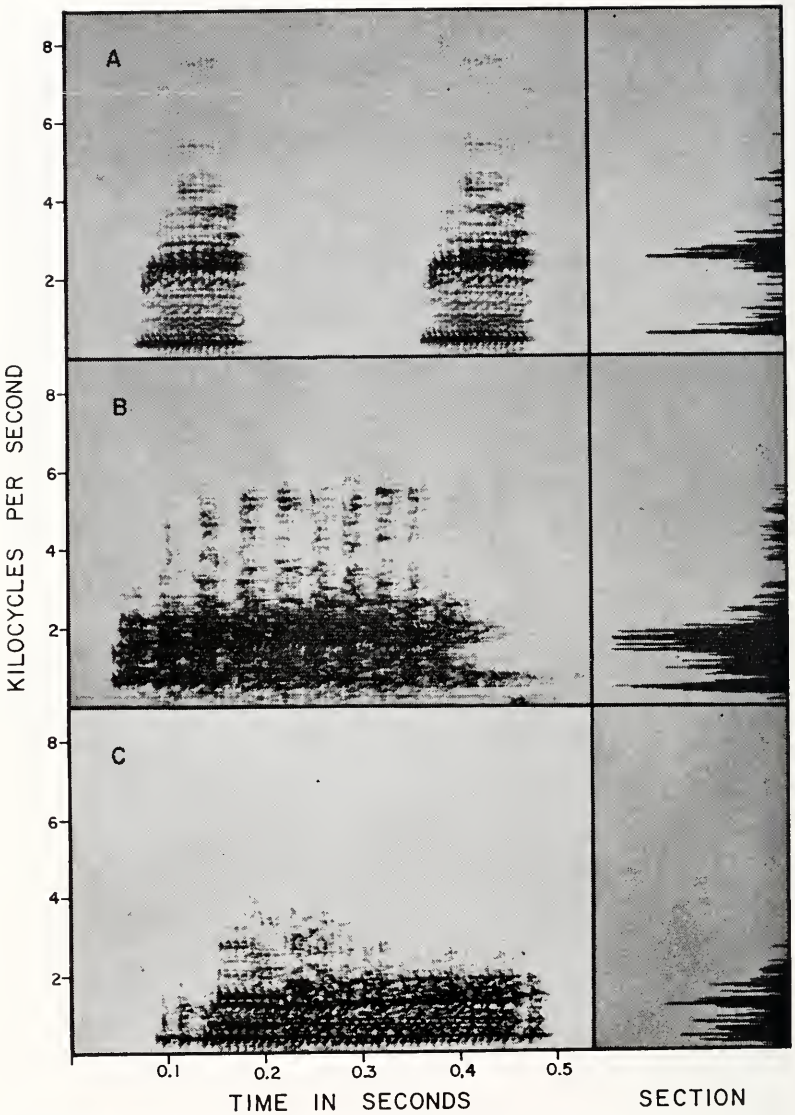
FIG. 2. Breeding site of *Smilisca phaeota*, Puerto Viejo, Heredia Prov., Costa Rica.

PLATE 9

FIG. 1. Breeding site of *Smilisca puma*, 7.5 km. W of Puerto Viejo, Heredia Prov., Costa Rica.

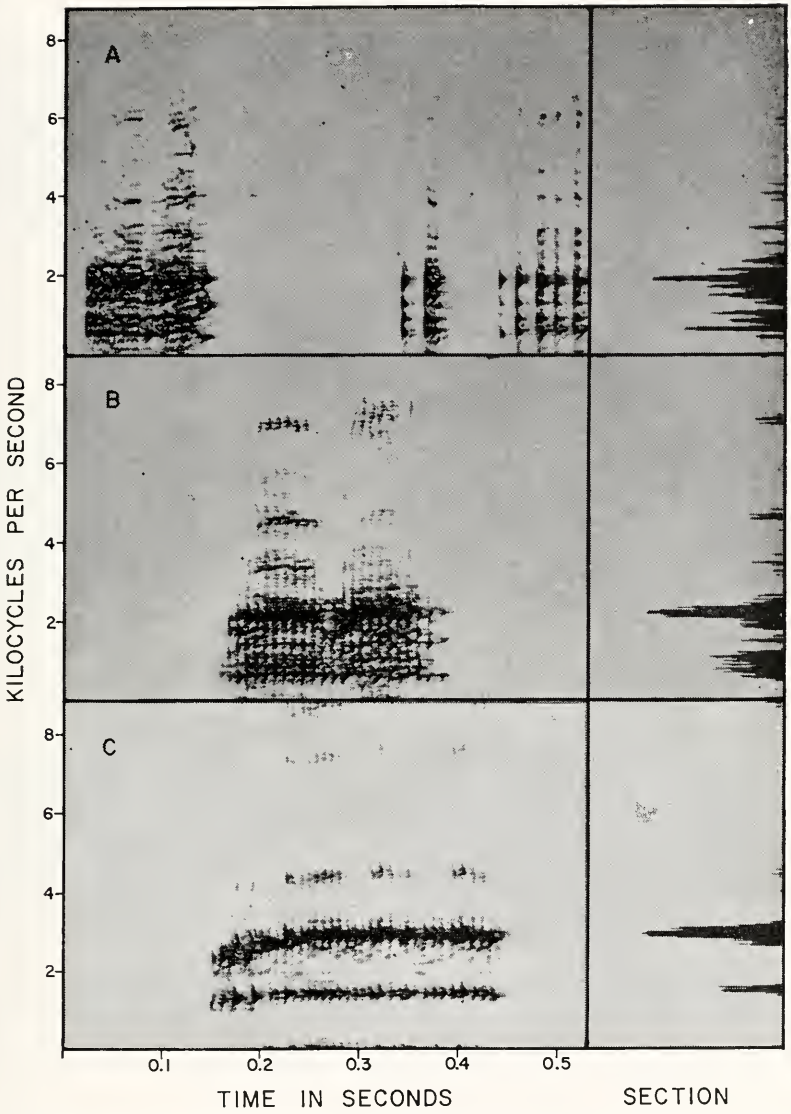
FIG. 2. Breeding site of *Smilisca sordida*, Río La Vieja, 30 km. E of Palmar Norte, Puntarenas Prov., Costa Rica.

PLATE 10



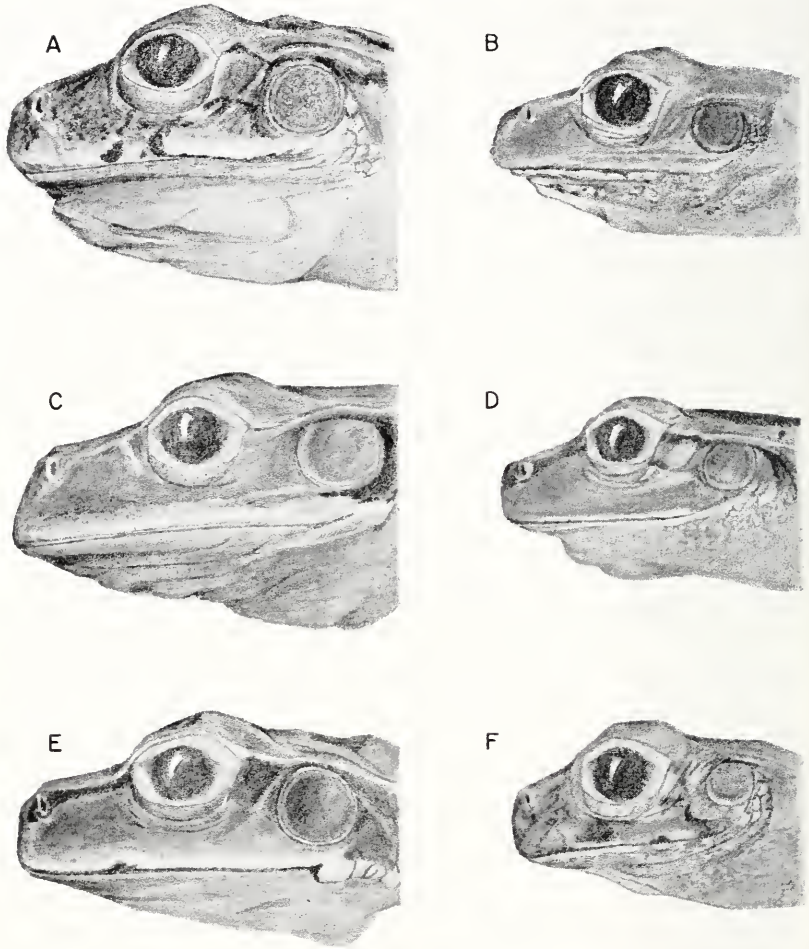
Audiospectrographs and sections of breeding calls of *Smilisca:* (A) *S. baudini* (KU Tape No. 74); (B) *S. cyanosticta* (KU Tape No. 373); (C) *S. phaeota* (KU Tape No. 79).

PLATE 11



Audiospectrographs and sections of breeding calls of *Smilisca:* (A) *S. puma* (KU Tape No. 382); (B) *S. sila* (KU Tape No. 385); (C) *S. sordida* (KU Tape No. 398).

PLATE 12



Lateral views of the heads of *Smilisca:* (A) *S. baudini* (KU 87177); (B) *S. sordida* (KU 91765); (C) *S. phaeota* (KU 64276); (D) *S. puma* (KU 91716); (E) *S. cyanosticta* (KU 87199); (F) *S. sila* (KU 77408). $\times 3.2$.

for a skeleton that he employed as the basis for the cranial characters diagnostic of the genus *Smilisca*, as defined by him. Although we cannot be certain, Cope apparently inadvertently used *daulinia* for *baudini*, just as he used *daudinii* for *baudini* (1871:205). Brocchi (1877:125) named *Hyla pansosana* from Panzos, Alta Verapaz, Guatemala.

Aside from the skeleton referred to as *Smilisca daulinia* by Cope (1865:194), we have examined each of the types of the species synonymized with *S. baudini*. All unquestionably are representatives of *S. baudini*.

Taylor (1942:306) named *Hyla beltrani* from Tapachula, Chiapas. This specimen (UIMNH 25046) is a small female (snout-vent length, 44 mm.) of *S. baudini*. Taylor (1954:630) named *Hyla manisorum* from Batán, Limón, Costa Rica. The type (KU 34927) is a large female (snout-vent length, 75.3 mm.) *S. baudini*. In this specimen and a male from Suretka, Costa Rica, the usual dorsal color pattern is absent, but the distinctive curved supraorbital processes, together with other structural features, show that the two specimens are *S. baudini*.

Hyla baudini dolomedes Barbour (1923:11), as shown by Dunn (1931a: 413), was based on a specimen of *Smilisca phaeota* from Río Esnápe, Darién, Panamá.

Distribution.—*Smilisca baudini* inhabits lowlands and foothills usually covered by xerophytic vegetation or savannas, but in the southern part of its range *baudini* inhabits tropical evergreen forest. The species ranges throughout the Pacific and Atlantic lowlands of México from southern Sonora and the Río Grande embayment of Texas southward to Costa Rica, where on the Pacific lowlands the range terminates at the southern limits of the arid tropical forest in the vicinity of Esparta; on the Caribbean lowlands the distribution

FIG. 1. Map showing locality records for *Smilisca baudini*.

seems to be discontinuous southward to Suretka (Fig. 1). Most localities where the species has been collected are at elevations of less than 1000 meters. Three localities are notably higher; calling males were found at small temporary ponds in pine-oak forest at Linda Vista, 2 kilometers northwest of Pueblo Nuevo Solistahuacán, Chiapas, elevation 1675 meters, and 10 kilometers northwest of Comitán, Chiapas, at an elevation of 1925 meters. Tadpoles and metamorphosing young were obtained from a pond in arid scrub forest, 17 kilometers northeast of Juchatengo, Oaxaca, elevation 1600 meters. Stuart (1954:46) recorded the species at elevations up to 1400 meters in the southeastern highlands of Guatemala.

Specimens examined.—3006, as follows: United States: Texas: Cameron County, Brownsville, CNHM 5412-3, 6869, UMMZ 54036, USNM 3256.

Mexico: **Campeche:** Balchacaj, CNHM 102285, 102288, 102291, 102311, UIMNH 30709-22, 30726; Champotón, UMMZ 73172 (2), 73176, 73180; 16 km. E Champotón, UMMZ 73181; 5 km. S Champotón, KU 71369-75; 9 km. S Champotón, KU 71367-8; 10.5 km. S Champotón, KU 71365-6, 71722 (tadpoles), 71723 (yg.); 24 km. S Champotón, UMMZ 73177 (2); Chuina, KU 75101-3; Ciudad del Carmen, UIMNH 30703-8; Dzibalchén, KU 75413-31; Encarnación, CNHM 102282, 102289, 102294-5, 102300, 102306-8, 102312, 102314, 102316-7, 102319, 102322, UIMNH 30727-40, 30836-7; 1 km. W Escárcega, KU 71391-6; 6 km. W Escárcega, KU 71397-403; 7.5 km. W Escárcega, KU 71376-89; 14 km. W Escárcega, KU 71390; 13 km. W, 1 km. N Escárcega, KU 71404; 3 km. N Hopelchén, KU 75410-11; 2 km. NE Hopelchén, KU 75412; Matamoras, CNHM 36573; Pitál, UIMNH 30741; 1 km. SW Puerto Real, Isla del Carmen, KU 71345-64; San José Carpizo, UMMZ 99879; Tres Brazos, CNHM 102284, UIMNH 30723-5; Tuxpeña Camp, UMMZ 73239.

Chiapas: Acacoyagua, USNM 114487-92; 2 km. W Acacoyagua, USNM 114493-4; 5 km. E Arroyo Minas, UIMNH 9533-7; Berriozabal, UMMZ 119186(7); Chiapa de Corzo, UMMZ 119185 (2); Cintalapa, UIMNH 50077; Colonia Soconusco, USNM 114495-9; 5 km. W Colonia Soconusco, UMMZ 87885 (7); Comitán, UMMZ 94438; 10 km. NW Comitán, KU 57185; El Suspiro, UMMZ 118819 (11); Escuintla, UMMZ 88271 (7), 88278, 88327, 109233; 6 km. NE Escuintla, UMMZ 87856 (26); 3 km. E Finca Juárez, UIMNH 9538; Finca Prussia, UMMZ 95167; Honduras, UMMZ 94434-7; La Grada, UMMZ 87862; 21 km. S La Trinitaria, UIMNH 9540-1; 14.4 km. SW Las Cruces, KU 64239-44; Palenque, UIMNH 49286, USNM 114473-84; 2 km. NW Pueblo Nuevo Solistahuacán, KU 57182-4, UMMZ 119948 (8), 121514; 1.3 km. N Puerto Madero, KU 57186-9; 4 km. N Puerto Madero, KU 57190-1; 8 km. N Puerto Madero, UMMZ 118379 (2); 12 km. N Puerto Madero, KU 57192; 17.6 km. N Puerto Madero, UMMZ 118378; Rancho Monserrata, UIMNH 9531-2, UMMZ 102266-7; Region Soconusco, UIMNH 33542-56; San Bartola, UIMNH 9519-30; San Gerónimo, UIMNH 30804; San Juanito, USNM 114485-6; San Ricardo, CNHM 102406; Solosuchiapa, KU 75432-3; Tapachula, CNHM 102208, 102219, 102239, 102405, UIMNH 25046, 30802-3; Tonolá, AMNH 531, CNHM 102232, 102416, UIMNH 30805-9, USNM 46760; Tuina, KU 41593 (skeleton); Tuxtla Gutierrez, CNHM 102231, 102248; 6 km. E Tuxtla Gutierrez, UIMNH 9539; 10 km. E Tuxtla Gutierrez, UMMZ 119949.

Chihuahua: 2.4 km. SW Toquina, KU 47226-7; Riito, KU 47228.

Coahuila: mountain near Saltillo, UIMNH 30833-4.

Colima: No specific locality, CNMH 1632; Colima, AMNH 510-11; Hacienda Albarradito, UMMZ 80029 (2); Hacienda del Colomo, AMNH 6208; Los Mezcales, UMMZ 80028; Manzanillo, AMNH 6207, 6209; Paso del Río, CNHM 102207, 102229-30, UIMNH 30819-21, UMMZ 110875 (3); Periquillo, UMMZ 80025 (3), 80026 (14); 1.6 km. SW Pueblo Juárez, UMMZ 115564; Queseria, CNHM 102204, 102216-7, 102224, UIMNH 30816-8, UMMZ 80023 (7), 80024 (7); Santiago, UMMZ 80027; 7.2 km. SW Tecolapa, UMMZ 115184.

Guerrero: Acahuizotla, UF 1338 (2), 1339-40, UMMZ 119182 (2), 119184; 3 km. S Acahuitzotla, KU 87183-7; Acapulco, AMNH 55276, UMMZ 121879 (4), USNM 47909; 3 km. N Acapulco, UMMZ 110127; 8 km. NW Acapulco, UF 11203 (7); 27 km. NE Acapulco, UIMNH 26597-610; Agua del Obispo, CNHM 102214, 102290, 102293, 102310, 102413, KU 60413, 87180-2, UIMNH 30764-6; Atoyca, KU 87175-8; Buena Vista, CNHM 102279, 102304, 102313, 102315, UIMNH 30774; Caculutla, KU 87179; 20 km. S Chilpancingo, CNHM 102242, 102401, 102410-1, 102415; Colonia Buenas Aires, UMMZ 119189; El Limoncito, CNHM 102292, 102303, 102321, 102414; El Treinte, CNHM 102212, 102221, 102237, 102240-1, UIMNH 30783-5, USNM 114508-10; Laguna Coyuca, UMMZ 80960 (2); 3 km. N Mazatlán, UIMNH 30777-9; 9 km. S Mazatlán, CNHM 102209, 102215, 102234, 102246, UIMNH 30781-2; Mexcala, CNHM 102399, 102403, 102409, 106539-40, UIMNH 30775-6; Ocotito, KU 60414-23; 5.4 km. N Ocotito, UMMZ 119181 (4); 1.6 km. N Organos, UIMNH 30752-63; Palo Blanco, CNHM 102283, 102286, 102305, 102320, 102404, UIMNH 30767-70; Pie de la Cuesta, AMNH 55275, 59202-5; Puerto Marquéz, AMNH 59200-1 (13); 5.6 km. S San Andreas de la Cruz, KU 87173-4; San Vincente, KU 87172; Zaculapán, UMMZ 119183.

Hidalgo: Below Tianguistengo, CNHM 102318.

Jalisco: Atenqueque, KU 91435-6; 5 km. NE Autlán, UIMNH 30810; 5 km. E Barro de Navidad, UMMZ 110900; Charco Hondo, UMMZ 95247; Puerto Vallarta, UIMNH 41346; between La Huerta and Tecomates, KU 91437; 3 km. SE La Resolana, KU 27619, 27620 (skeleton); 11 km. S, 1.6 km. E Yahualica, KU 29039; Zapotilitic, CNHM 102238.

Michoacán: Aguililla, UMMZ 119179 (5); Apatzingán, CNHM 38766-90, KU 69101 (skeleton); 7 km. E Apatzingán, UMMZ 112843; 11 km. E Apatzingán, UMMZ 112841 (3); 27 km. S Apatzingán, KU 37621-3; 1.6 km. N Arteaga, UMMZ 119180; Charapendo, UMMZ 112840; Coahuayana, UMMZ 104458; El Sabino, CNHM 102205-6, 102210-1, 102220, 102228, 102233, UIMNH 30822-3; La Placita, UMMZ 104456; La Playa, UMMZ 105163; 30 km. E Nueva Italia, UMMZ 120255 (2); 4 km. S Nueva Italia, UMMZ 112842; Ostula, UMMZ 104457 (4); Salitre de Estopilas, UMMZ 104459; San José de la Montaña, UMMZ 104461 (2); 11 km. S Tumbiscatio, KU 37626; 12 km. S Tzitzio, UMMZ 119178.

Morelos: 3.5 km. W Cuautlixco, KU 87188-90; 1 km. NE Puente de Ixtla, KU 60393-4; 20 km. S Puente de Ixtla, CNHM 102400, UIMNH 30832; Tequesquitengo, AMNH 52036-9.

Nayarit: 3 km. S Acaponeta, UMMZ 123030 (4); 56 km. S Esquinapa (Sinaloa), KU 73909; Jesús María, AMNH 58239; San Blas, KU 28087, 37624, 62360-2, USNM 51408; 8.6 km. E San Blas, UMMZ 115185; Tepic, UIMNH 30812-5; 4 km. E Tuxpan, KU 67786; 11 km. SE Tuxpan, UIMNH 7329-31, 7335-59.

Nuevo León: Galeana, CNHM 34389; Salto de Cola de Caballo, CNHM 30628-31, 30632 (40), 30633-7, 34454-67.

Oaxaca: 11 km. S Candelaria, UIMNH 9515-8; Cerro San Pedro, 24 km. SW Tehuantepec, UMMZ 82156; Chachalapa, KU 38199; 8 km. S Chiltepec, KU 87191; 12 km. S Chivela, UMMZ 115182; Coyul, USNM 114512; Garza Mora, UIMNH 40967-8; Juchatengo, KU 87193; 17 km. NE Juchatengo, KU 87645 (tadpoles), 87646 (young); Juchitán, USNM 70400; Lagartero, UIMNH 9514; Matiás Romero, AMNH 52143-5; 25 km. N Matías Romero, KU 33822-8; 7 km. S Matías Romero, UIMNH 42703; Mirador, AMNH 6277, 13832-9, 13842-55; Mira León, 1.6 km. N Huatulco, UIMNH 9503-4; Mixtequillo, AMNH 13924; Pochutla, KU 57167-81, UIMNH 9505-13; Quiengola, AMNH 51817, 52146; Río del Corte, UIMNH 48677; Río Mono Blanco, UIMNH 36831; Río Sarabia, 5 km. N Sarabia, UMMZ 115180 (4); 2.5 km. N Salina Cruz, KU 57165-6; San Antonio, UIMNH 37286; 5 km. NNW San Gabriel Mixtepec, KU 87192; San Pedro del Istmo, UIMNH 37197; Santo Domingo, USNM 47120-2; 3.7 km. N Sarabia, UMMZ 115181 (3); Tapanatepec, KU 37793 (skeleton), 37794, UIMNH 9542, UMMZ 115183; between Tapanatepec

and Zanatepec, UIMNH 42704-25; Tecuane, UMMZ 82163 (3); Tehuantepec, AMNH 52625, 52639, 53470, UMMZ 82157-8, 82159 (9), 82160 (4), 82161 (8), 82162 (12), 112844-5, 118703, USNM 10016, 30171-4, 30188; 4.5 km. W Tehuantepec, KU 59801-12 (skeletons), 69102-3 (skeletons); 10 km. S Tehuantepec, KU 57163-4; Temazcal, USC 8243 (3); 3 km. S Tolocita, KU 39666-9; Tolosa, AMNH 53605; Tuxtepec, UMMZ 122098 (2); 2 km. S Valle Nacional, KU 87194-5; 11 km. N Vista Hermosa, KU 87196, 87639-41 (tadpoles), 87642-3 (young), 87644 (tadpoles); Yetla, KU 87197.

Puebla: 16 km. SW Mecatepec (Veracruz), UIMNH 3657-8; San Diego, AMNH 57714, USNM 114511; Vegas de Suchil, AMNH 57712; Villa Juárez, UF 11205.

Quintana Roo: Cóba, CNHM 26937; Esmeralda, UMMZ 113551; 4 km. NNE Felipe Carrillo Puerto, KU 71417-8; Pueblo Nuevo X-Can, KU 71405; 10 km. ENE Pueblo Nuevo X-Can, KU 71406; 4 km. WSW Puerto Juárez, KU 71407-11, 71721 (tadpoles); 12 km. W Puerto Juárez, KU 71412-6; San Miguel, Isla de Cozumel, UMMZ 78542 (6), 78543 (10), 78544 (2); 3.5 km. N San Miguel, Isla de Cozumel, KU 71419-22; 10 km. E San Miguel, Isla de Cozumel, UMMZ 78541; Telantunich, CNHM 26950.

San Luis Potosí: Ciudad Valles, AMNH 57776-81 (12), CNHM 37193, 102297, KU 23705; 21 km. N Ciudad Valles, UMMZ 118377; 6 km. E Ciudad Valles, UF 3524; 24 km. E Ciudad Valles, UF 7340 (2); 5 km. S Ciudad Valles, UIMNH 30751; 16 km. S Ciudad Valles, AMNH 52953; 30 km. S Ciudad Valles, CNHM 102394, 102402, 102412, UIMNH 30749-50; 63 km. S Ciudad Valles, UIMNH 19247-58; Pujal, UMMZ 99872 (2); Río Axtla, near Axtla, AMNH 53211-5, 59516, KU 23706; Tamazunchale, AMNH 52675, CNHM 39621-2, 102226, 102281, UF 7615 (2), UIMNH 26596, UMMZ 99506 (9), 118701 (2), USNM 114468; 17 km. N Tamazunchale, UIMNH 3659; 2.4 km. S Tamazunchale, AMNH 57743; 17 km. E Tamuin, UF 11202 (2); Xilitla, UIMNH 19259-60.

Sinaloa: 8 km. N. Carrizalejo, KU 78133; 4 km. NE Concordia, KU 73914; 5 km. SW Concordia, KU 75438-9; 6 km. E Cosalá, KU 73910; Costa Rica, 16 km. S. Culiacán, UIMNH 34887-9; 51 km. SSE Culiacán, KU 37792; El Dorado, KU 60392; 1.6 km. NE El Fuerte, CNHM 71468; Isla Palmito del Verde, middle, KU 73916-7; 21 km. NNE Los Mochis, UIMNH 40536-7; Matatán, KU 73913; 7.3 km. SW Matatán, KU 78464, 78466-70; Mazatlán, AMNH 12562, UMMZ 115197 (3); 57 km. N Mazatlán, UIMNH 38364; Plomosas, USNM 47439-40; Presidio, UIMNH 30811, USNM 14082; Rosario, KU 73911-2; 5 km. E Rosario, UIMNH 7360-76; 8 km. SSE Rosario, KU 37625; 5 km. SW San Ignacio, KU 78465; 1.6 km. ENE San Lorenzo, KU 47917-24; Teacapán, Isla Palmito del Verde, KU 73915; 9.6 km. NNW Teacapán, KU 91410; Villa Unión, KU 78471; 9 km. NE Villa Unión, KU 75434-7; 1 km. W Villa Unión, AMNH 59284.

Sonora: Guiracoba, AMNH 51225-38 (25).

Tabasco: 4 km. NE Comalcalco, AMNH 60313; Teapa, UMMZ 119943; 5 km. N Teapa, UMMZ 119940, 119944, 122997 (2); 10 km. N Teapa, UMMZ 119187, 119188 (2); 13 km. N Teapa, UMMZ 119941 (2), 119945 (3), 120254 (2); 21 km. N Teapa, UMMZ 119942, 119947; 29 km. N Teapa, UMMZ 119946 (11); Tenosique, USNM 114505-7.

Tamaulipas: Acuña, UMMZ 99864; 5 km. S Acuña, UMMZ 101180; 13 km. N Antiguo Morelos, UIMNH 40532-5; 3 km. S Antiguo Morelos, UF 11204; 3 km. NE Chamal, UMMZ 102867; 1.6 km. E Chamal, UMMZ 110734; Ciudad Mante, UMMZ 80957, 80958 (3), 106400 (3); 16 km. N Ciudad Victoria, CNHM 102408; 34 km. NE Ciudad Victoria, KU 60395-411; 8.8 km. S Ciudad Victoria, UIMNH 19261-3; 11 km. W Ciudad Victoria, UIMNH 30924; 16 km. W Ciudad Victoria, UIMNH 30825; 3 km. W El Carizo, UMMZ 111279; Gómez Farías, UMMZ 110837-8; 8 km. NE Gómez Farías, UMMZ 102265, 102916 (4), 102917, 104110 (5), 105493, 110836 (2), 111274-7; 8 km. NW Gómez Farías, UMMZ 101178 (7), 101179 (3), 101362-3, 101364 (2), 108799 (2), 110129, 111278, 111280; 8 km. W Gómez Farías, UMMZ 102859 (2); 16 km. W Gonzales, KU 37795-6; Jiménez, KU 60412; La Clementina, 6 km.

W Forlan, USNM 106244; Limón, UIMNH 30831; Llera, USNM 140137-40; 3 km. E Llera, UIMNH 16858; 21 km. S Llera, UIMNH 30828-9; 23 km. S Llera, UIMNH 30830; 11 km. SW Ocampo, UMMZ 118956; 22 km. W, 5 km. S Piedra, KU 37568-71; Rio Sabinas, UMMZ 97976; 5 km. W San Gerardo, UMMZ 110733 (2); Santa Barbara, UMMZ 111272-3; Villagrán, CNHM 102280, 102287, 102299, 102309, UIMNH 30826-7; 1.7 km. W Xicotencatl, UMMZ 115179.

Veracruz: 1.6 km. NW Acayucan, UMMZ 115189; 28.5 km. SE Alvarado, UMMZ 119933; 2.4 km. SSW Amatitlán, UMMZ 115195; Barranca Metlac, UIMNH 38365; Boca del Río, UIMNH 26619-30, UMMZ 74954 (9); 16 km. S Boca del Río, UIMNH 26631; between Boca del Río and Anton Lizardo, UIMNH 42701; Canadá, CNHM 102397; Catemaco, UMMZ 118702 (4); Ciudad Alemán, UMMZ 119608 (3); Córdoba, CNHM 38665-7, USNM 30410-3; 5.2 km. ESE Córdoba, KU 71423-35, 89924 (skeleton); 7 km. ESE Córdoba, UMMZ 115176 (4); Cosamaloapan, UMMZ 115193 (2); Coyame, UIMNH 36853-6, 38366, UMMZ 111461 (3), 111462-3; 1 km. SE Coyame, UMMZ 121202 (3); Cuatotolapam, UMMZ 41625-39; Cuautlapan, CNHM 38664, 70591-600, 102218, 102398, KU 26300, 26302, 26309, 26312-3, 26315-6, 26321, 26336, 26339, 26347 (skeleton), 26354, 55614-21 (skeletons), UIMNH 11236-67, 11269-71, 11273, 26611-8, 30792-5, UMMZ 85466 (6), 115173 (25), 115175 (7), USNM 114433-57; Dos Ríos, CNHM 39623; 5 km. ENE El Jobo, KU 23843, 23845, 23847; 6.2 km. E Encero, UIMNH 30835; Escamilo, CNHM 102298, UIMNH 30788; 1 km. N Fortín, UF 11201; 4 km. SW Huatusco, UMMZ 115177; 1 km. SW Huatusco, UMMZ 123119; 10 km. SE Hueyapan, UMMZ 115190; 20 km. S Jesús Carranza, KU 23844, 23846, 27399; 38 km. SE Jesús Carranza, KU 23417; Laguna Catemaco, UMMZ 119932 (62); 1.6 km. N La Laja, UIMNH 3651; La Oaxaqueña, AMNH 43930-1; 17 km. E Martínez de la Torre, UIMNH 36630-2; 6.2 km. W Martínez de la Torre, UIMNH 3652-4; Minatitlán, AMNH 52141-2; Mirador, USNM 25097-8, 115178; 6 km. S Monte Blanco, UF 11200 (4); 21 km. E Nanchital, UMMZ 123004; 2 km. S Naranja, UMMZ 115188 (3); 1.6 km. NE Novillero, UMMZ 115194 (2); 3 km. NE Novillero, UMMZ 115196; 5.2 km. NE Novillero, UMMZ 115192 (4); 6 km. NE Novillero, UMMZ 115191; 5 km. N Nuevo Colonia, UMMZ 105066; Orizaba, USNM 16563-6; 4 km. NE Orizaba, UMMZ 120251 (2); Panuco, UMMZ 118922; Paraje Nuevo, UMMZ 85465 (2), 85467 (35), 85468 (36); Paso del Macho, UIMNH 49281; Paso de Talaya, Jicaltepec, USNM 32365, 84420; Pérez, CNHM 1686 (5); 20 km. N Piedras Negras, Río Blanco, KU 23708; Plan del Río, KU 26310, 26333-5, 26345, 26354, UMMZ 102069, 102070 (5); Potrero, UIMNH 49282-5, UMMZ 88799, 88805, 88806 (2), USNM 32391-5; Potrero Viejo, CNHM 102296, KU 26301, 26304-5, 26307-8, 26311, 26317-20, 26323-25, 26326-8 (skeletons), 26329-31, 26332 (skeleton), 26337-8, 26340-4, 26346, 26348, 26351, 26353, 27400-12, UIMNH 30800, UMMZ 88800 (2), 88802 (15), 88803 (9), 88804, USNM 114458-67; 5 km. S Potrero Viejo, KU 26303, 26314, 26322; Puente Nacional, UIMNH 21783-8; 3 km. N Rinconada, UMMZ 122099 (5); Río de las Playas, USNM 118635-6; Río Seco, UMMZ 88801 (9); Rodriguez Clara, CNHM 102225; San Andrés Tuxtla, CNHM 102213, 102222, 102227, 102247, UIMNH 30789-91; 10 km. NW San Andrés Tuxtla, UMMZ 119935; 13.4 km. NW San Andrés Tuxtla, UMMZ 119939 (2); 19.8 km. NW San Andrés Tuxtla, UMMZ 119938; 27.2 km. NW San Andrés Tuxtla, UMMZ 119936 (6); 48 km. NW San Andrés Tuxtla, UMMZ 119937; 4 km. W San Andrés Tuxtla, UMMZ 115187; 37.4 km. S San Andrés Tuxtla, UMMZ 119934 (12); 15 km. ESE San Juan de la Punta, KU 23707; San Lorenzo, USNM 123508-12; 3 km. SW San Marcias, KU 23841; 1.5 km. S Santa Rosa, UIMNH 42702; 2 km. S Santiago Tuxtla, UMMZ 121201 (4); Sauzel, UMMZ 121239; 14 km. E Suchil, UIMNH 46880; 15 km. S Tampico (Tamaulipas), UMMZ 103322 (4); 4 km. N Tapalapan, UMMZ 115186 (2); Tecolutla, UIMNH 42677-700; 16 km. NW Tehuatlán, UIMNH 3660-3; 5 km. S Tehuatlán, KU 23842; Teocelo, KU 26306; Tierra Colorado, CNHM 102393, 102395-6, UIMNH 30789-91; Veracruz, AMNH 6301-4, 59398-402, UIMNH 30801, UMMZ 115174, 122060 (2); 24 km. W Veracruz, CNHM 104570-2.

Yucatán: No specific locality, CNHM 548, 49067, USNM 32298; Chichén-Itzá, CNHM 20636, 26938-49, 36559-62, UIMNH 30742-6, UMMZ 73173 (6), 73174 (14), 73175 (14), 73178-9, 76171, 83107 (2), 83108, 83109 (2), 83915 (30), USNM 72744; 9 km. E Chichén-Itzá, KU 71438-9; 12 km. E Chichén-Itzá, KU 71440; Mérida, CNHM 40659-66, UIMNH 30747-8, UMMZ 73182; 6 km. S Mérida, KU 75194; 8.8 km. SE Ticul, UMMZ 114296; Valladolid, CNHM 26934-6; Xcalah-op, CNHM 53906-14; 3.5 km. E Yokdzonot, KU 71441-3, 71720 (tadpoles).

British Honduras: Belize, CNHM 4153, 4384-5, 4387, UMMZ 75310, USNM 26065; Bokowina, CNHM 49064-5; Cocquercote, UMMZ 75331 (2); Cohune Ridge, UMMZ 80738 (15); Double Falls, CNHM 49066; El Cayo, UMMZ 75311; 6 km. S El Cayo, MCZ 37856; Gallon Jug, MCZ 37848-55; Manatee, CNHM 4264-7; Mountain Pine Ridge, MCZ 37857-8; San Augustin, UMMZ 80739; San Pedro, Columbia, MCZ 37860-2; Valentin, UMMZ 80735 (4), 80736 (2), 80737 (2); 5 km. S Waha Loaf Creek, MCZ 37859.

Guatemala: **Alta Verapaz:** 5.1 km. NE Campur, KU 68464 (tadpoles), 67465 (young); 28.3 km. NE Campur, KU 64203-22, 68183-4 (skeletons); Chamá, MCZ 15792-3, UMMZ 90895 (7), 90896 (5), 90897 (29), 90898 (12), 90899; Chinajá, KU 55939-41, 57193-8, 60018-20 (tadpoles), 60021 (eggs), 60022 (tadpoles); Cobán, CNHM 21006; Cubilquitz, UMMZ 90902 (10); Finca Canihor, UMMZ 90908; Finca Chicoyou, KU 57246-8, 60026 (young), 64202, 68466-7 (tadpoles); Finca Los Alpes, KU 64197-201, 68463 (tadpoles); Finca Los Pinales, UMMZ 90903 (2); Finca Tinajas, BYU 16031; Finca Volcán, UMMZ 90905 (4), 90906-7; Panzos, MNHN 6313, UMMZ 90904; Samac, UMMZ 90900; Samanzana, UMMZ 90901 (6).

Baja Verapaz: Chejel, UMMZ 90909 (7), 90910 (3); San Gerónimo, UMMZ 84076 (16).

Chiquimula: 1.6 km. SE Chiquimula, UMMZ 98112; Esquipulas, UMMZ 106793 (28).

El Petén: 20 km. NNW Chinajá (Alta Verapaz), KU 57199-240; Flores, UMMZ 117985; La Libertad, KU 60024 (young), UMMZ 75313-20, 75323 (2), 75324 (7), 75325 (13), 75326 (2), 75327 (11), 75328 (12), 75329 (2); 3 km. SE La Libertad, KU 57243-4; 13 km. S La Libertad, MCZ 21458 (2); Pacomon, USNM 71334; Piedras Negras, USNM 114469-71; Poptún, UMMZ 120475; Poza de la Jicotea, USNM 114672; Ramate-Yaxha trail, UMMZ 75321; Río de la Pasión between Sayaxché and Subín, KU 57151; Río San Román, 16 km. NNW Chinajá (Alta Verapaz), KU 55942-6; Sacluc, USNM 25131; Sayaxché, KU 57144-5; Tikal, UMMZ 117983 (7), 117984 (5), 117993 (5), 120474 (5); Toocog, KU 57241-2, 60023 (young), 60025 (young); Uaxactún, UMMZ 70401-3; Yaxha, UMMZ 75322; 19 km. E Yaxha, UMMZ 75330 (4).

El Quiché: Finca Tesoro, UMMZ 89166 (3), 90549 (tadpoles).

Escuintla: Río Guacalate, Masagua, USNM 125239; Tiquisate, UMMZ 98262 (7).

Guatemala: 16 km. NE Guatemala, KU 43545-53.

Huehuetenango: Finca San Rafael, 16 km. SE Barillas, CNHM 40912-6; 45 km. WNW Huehuetenango, KU 64223-4; Jacaltenango, UMMZ 120080 (6), 120081 (14), 120082 (13).

Izabál: 2 km. SW Puerto Matías de Gálvez, KU 60027-8 (tadpoles); Quiriguá, CNHM 20587, UMMZ 70060.

Jalapa: Jalapa, UMMZ 98109, 106792 (11).

Jutiapa: Finca La Trinidad, UMMZ 107728 (10); Jutiapa, UMMZ 106789; 1.6 km. SE Mongoy, KU 43069; Santa Catarina Mita, UMMZ 106790.

Progreso: Finca Los Leones, UMMZ 106791.

Quetzaltenango: Coatepeque, AMNH 62204.

Retalhueleu: Casa Blanca, UMMZ 107725 (18); Champerico, UMMZ 107726 (3).

San Marcos: Talisman Bridge, USNM 128056-7.

Santa Rosa: Finca La Guardiana, UMMZ 107727 (6); Finca La Gloria, UMMZ 107724 (6); 1.6 km. WSW El Molino, KU 43065-8.

EL SALVADOR: La Libertad: 16 km. NW Santa Tecla, KU 43542-4. Morazán: Divisadero, USNM 73284. San Salvador: San Salvador, CNHM 65087-99, KU 61955-88, 62138-9 (skeletons), 62154 (eggs), 62155-60 (tadpoles), 68462 (tadpoles), UMMZ 117586 (3), 118380 (3), USNM 140278.

HONDURAS: State unknown: Guaimas, UMMZ 58391. Atlantidad: Isla de Roatán, CNHM 34551-4; La Ceiba, USNM 64985, 117589-91; Lancetilla, MCZ 16207-11; Tela, MCZ 15774-5, 28080, UMMZ 58418, USNM 82173-4. Choluteca: 1.5 km. NW Choluteca, KU 64228-32; 10 km. NW Choluteca, KU 64233; 10 km. E Choluteca, KU 64226-7; 12 km. E Choluteca, KU 64225; 5 km. S Choluteca, USC 2700 (2). Colón: Bambú, UF 320; Belfate, AMNH 45692-5; Patuca, USNM 20261. Comayagua: La Misión, 3.5 leagues N Siguatepeque, MCZ 26424-5. Copán: Copán, UMMZ 83026 (2). Cortés: Cofradia, AMNH 45345-6; Hacienda Santa Ana, CNHM 4724-31; Lago de Yojoa, MCZ 26410-1; Río Lindo, AMNH 54972. El Paraiso: El Volcán, MCZ 26436. Francisco Morazán: Tegucigalapa, BYU 18301-4, 18837-41, MCZ 26395-7, USNM 60499. Gracias A Dios: Río Segovia, MCZ 24543. Santa Barbara: Santa Barbara, USNM 128062-5.

NICARAGUA: Chinandega: 4 km. N, 2 km. W Chichigalpa, KU 85385; Chinandega, MCZ 2632; Río Tama, USNM 40022; San Antonio, KU 84944-9 (skeletons), 85386-403. Chontales: 1 km. NE Acoyapa, KU 64234. Estelí: Finca Daraili, 5 km. N, 15 km. E Condega, KU 85404-8; Finca Venecia, 7 km. N, 16 km. E Condega, KU 85409. León: 1.6 km. ENE Poneloya, KU 43084-5. Managua: Managua, USNM 79989-90; 8 km. NW Managua, KU 43094-110; 20 km. NE Managua, KU 85412; 21 km. NE Managua, KU 85413-4; 5 km. SW Managua, KU 43086-93; 2 km. N Sabana Grande, KU 85411; 3 km. N Sabana Grande, KU 43070-8; 20 km. S, 0.5 km. W Tipitapa, KU 85410. Matagalpa: Guasqualie, UMMZ 116493; Matagalpa, UMMZ 116492; 19 km. N Matagalpa, UMMZ 116494. Río San Juan: Greytown, USNM 19585-6, 19767-8. Rivas: Javillo, UMMZ 123001; Moyogalpa, Isla Ometepe, KU 85428-37, 87706 (tadpoles); Peñas Blancas, KU 85417; Río Javillo, 3 km. N, 4 km. W Sapoá, KU 85418-20, 85438 (skeleton); 13.1 km. SE Rivas, KU 85415; 14.8 km. SE Rivas, KU 85421-3; 11 km. S, 3 km. E Rivas, KU 85416; 16 km. S Rivas, MCZ 29009-10; 7.7 km. NE San Juan del Sur, KU 85426-7; 16.5 km. NE San Juan del Sur, KU 85424-5, 87705 (young); 5 km. SE San Pablo, KU 43079-83. Zelaya: Cooley, AMNM 7063-8, 8019-20, 8022, 8034-5; Cukra, AMNH 8016-7; Musahuas, Río Huaspuc, AMNH 58428-31; 11 km. NW Rama, Río Siquia, UMMZ 79708, 79709 (5), 79710 (2); Río Escondido, USNM 19766, 20701; Río Siquia at Río Mico, UMMZ 79707 (10); Sioux Plantation, AMNH 7058-61, 8023-33.

COSTA RICA: Alajuela: Los Chiles, AMNH 54639; Orotina, MCZ 7960-1; San Carlos, USNM 29991. Guanacaste: La Cruz, USC 8232 (3); 4.3 km. NE La Cruz, UMMZ 123002; 18.4 km. S La Cruz, USC 8136; 23.5 km. S La Cruz, USC 8094 (4); 3 km. W La Cruz, USC 8233 (4); 2 km. NE Las Cañas, KU 64235-7; Las Huecas, UMMZ 71212-3; Liberia, KU 36787, USC 8161; 11.5 km. N Liberia, USC 8149; 13 km. N Liberia, USC 8139; 22.4 km. N Liberia, USC 8126; 8 km. NNW Liberia, KU 64238; 8.6 km. ESE Playa del Coco, USC 8137; 21.8 km. ESE Playa del Coco, USC 8138; Río Piedra, 1.6 km. W Bagaces, USC 7027; Río Bebedero, 5 km. S Bebedero, KU 64158; 5 km. NE Tilarán, KU 36782-6. Heredia: 13 km. SW Puerto Viejo, KU 64142-6. Limón: Batán, KU 34927; Guacimo, USC 621; Pandora, USC 505 (3); Suretka, KU 36788-9; Tortugero, UF 7697, 10540-2. Puntarenas: Barranca, CNHM 35254-6; 15 km. WNW Barranca, KU 64155-7, UMMZ 118381; 18 km. WNW Barranca, UMMZ 118382 (4); 4 km. WNW Esparta, KU 64159-96, 68178-82 (skeletons); 19 km. NW Esparta, KU 64147-54.

Smilisca cyanosticta (Smith), new combination

Hyla phaeota, Taylor, Univ. Kansas Sci. Bull., 28(5):80, May 15, 1942.
Taylor and Smith, Proc. U. S. Natl. Mus., 95(3185):589, June 30, 1945.

Hyla phaeota cyanostica Smith, Herpetologica, 8:150, Jan. 30, 1953 [Holotype.—USNM 111147 from Piedras Negras, El Petén, Guatemala; Hobart M. Smith collector]. Shannon and Werler, Trans. Kansas Acad. Sci., 58:386, Sept. 24, 1955. Poglayen and Smith, Herpetologica, 14:11, April 25, 1958. Cochran, Bull. U. S. Natl. Mus., 220:57, 1961. Smith, Illinois Biol. Mono., 32:25, May, 1964.

Smilisca phaeota cyanosticta, Stuart, Misc. Publ. Mus. Zool. Univ. Michigan, 122:42, April 2, 1963. Duellman, Univ. Kansas Publ. Mus. Nat. Hist., 15(5):229, Oct. 4, 1963.

Diagnosis.—Size moderately large (♂ 56.0 mm., ♀ 70.0 mm.); skull as long as wide; frontoparietal fontanelle large; narrow supraorbital flanges having irregular margins anteriorly; large squamosal not in contact with maxillary; tarsal fold moderately wide, full length of tarsus; inner metatarsal tubercle moderately large, low, flat, elliptical; hind limbs relatively long; tibia usually more than 52 per cent of snout-vent length; labial stripe silvery-white; lips lacking vertical bars; loreal region pale green; pale bronze-colored stripe from nostril along edge of eyelid to point above tympanum narrow, bordered below by narrow dark brown stripe from nostril to eye, and broad dark brown postorbital mark encompassing tympanum and terminating above insertion of arm; flanks, dark brown with large pale blue spots; anterior and posterior surfaces of thighs dark brown with small pale blue spots on thighs. (Foregoing combination of characters distinguishing *S. cyanosticta* from any other species in genus.)

Description and Variation.—The largest males are from Piedras Negras, El Petén, Guatemala, and they average 52.5 mm. in snout-vent length whereas males from Los Tuxtlas, Veracruz, average 50.6 mm. and those from northern Oaxaca 50.3 mm. The smallest breeding male has a snout-vent length of 44.6 mm. The average ratio of tibia length to snout-vent length is 54.8 per cent in males from Piedras Negras, and 56.4 and 56.3 per cent in males from Los Tuxtlas and Oaxaca, respectively. The only other character showing noticeable geographic variation is the size of the tympanum. The average ratio of the diameter of the tympanum to the diameter of the eye is 76.3 per cent in males from Piedras Negras, 71.8 from Oaxaca, and 66.9 from Los Tuxtlas.

The dorsal ground color of *Smilisca cyanosticta* is pale green to tan and the venter is creamy-white. The dorsum is variously marked with dark olive-green or dark brown spots or blotches (Pl. 6B). An interorbital dark bar usually is present. The most extensive dark area is a V-shaped mark in the occipital region with the anterior branches not reaching the eyelids; this mark is continuous, by means of a narrow mid-dorsal mark, with an inverted V-shaped mark in the sacral region. In many specimens this dorsal marking is interrupted, resulting in irregular spots. In some specimens the dorsum is nearly uniform pale green or tan with a few small, dark spots. The hind limbs are marked by dark transverse bands, usually three or four each on the thigh and shank, and two or three on the tarsus. The webbing on the feet is brown. The loreal region is pale green, bordered above by a narrow, dark brown canthal stripe extending from the nostril to the orbit, which is bordered above by a narrow, bronze-colored stripe extending from the nostril along the edge of the eyelid to a point above the tympanum. The upper lip is white. A broad dark brown mark extends posteriorly from the orbit and encompasses the tympanum to a point above the insertion of the forelimb. The flanks are dark brown with many pale blue, rounded spots, giving the impression of a pale

blue ground color with dark brown mottling enclosing spots. The anterior and posterior surfaces of the thighs are dark brown with many small pale blue spots. The inner surfaces of the shank and tarsus are colored like the posterior surfaces of the thighs. Pale blue spots are usually present on the proximal segments of the second and third toes. A distinct white stripe is present on the outer edge of the tarsus and fifth toe; on the tarsus the white stripe is bordered below by dark brown. A white stripe also is present on the outer edge of the forearm and fourth finger. The anal region is dark brown, bordered above by a narrow transverse white stripe. The throat in breeding males is dark, grayish brown with white flecks.

No geographic variation in the dorsal coloration is evident. Specimens from the eastern part of the range (Piedras Negras and Chinajá, Guatemala) have bold, dark reticulations on the flanks enclosing large pale blue or pale green spots, which fade to tan in preservative. Specimens from Oaxaca and Veracruz characteristically have finer dark reticulations on the flanks enclosing smaller blue spots; in many of these specimens the ventrolateral spots are smallest and are white.

All living adults are easily recognized by the presence of pale, usually blue, spots on the flanks and thighs. Individuals under cover by day have a tan dorsum with dark brown markings. A hiding individual at Chinajá, Alta Verapaz, Quatemala (KU 55936), had a pale tan dorsum when found; later the dorsal color changed to chocolate brown. A pale green patch was present below the eye; the spots on the posterior surfaces of the thighs were pale blue, and those on the flanks were yellowish green. A calling male obtained 10 kilometers north-northwest of Chinajá (KU 55934) was reddish brown when found at night; later the dorsal color changed to pale tan. A green patch below the eye was persistent. Usually these frogs are green at night. The coloration of an adult male (KU 87201) from 11 kilometers north of Vista Hermosa, Oaxaca, México, was typical: "When calling dorsum pale green; later changed to dull olive-green. Flanks dark brown with pale blue spots in axilla and groin and bluish white flecks on mid-flank. Anterior and posterior surfaces of thighs, inner surfaces of shanks, and median dorsal surfaces of tarsi dark brown with blue spots. Canthal and postorbital stripes dark chocolate brown; labial stripe creamy white. Forearm, tarsal, and anal stripes pale cream-color. Throat dark brown with yellow flecks; belly and ventral surfaces of limbs creamy buff; webs pinkish tan; iris deep bronze, brown below pupil." (Duellman, field notes, June 24, 1964.)

Some individuals have both green and brown coloration in life. An individual obtained at night on the south slope of Volcán San Martín, Veracruz, México, had a pale tan dorsum changing peripherally to pale green. The dorsal markings were dark brown and dark olive-green.

In contrast to the color-changes noted above, the labial region below the eye is always pale green, and pale spots are always present on the flanks and thighs in adults. The iris is invariably golden or bronze above and darker, usually brown, below. Minute black flecks are present on the iris, and in some individuals these flecks are so numerous that the eye appears gray.

Recently metamorphosed young have pale tan flanks, and the posterior surfaces of the thighs are orange-yellow; pale spots are absent. A juvenile (KU 55935) from Chinajá, Alta Verapaz, Guatemala, having a snout-vent length of 35.0 mm. was pale yellowish tan above with olive-green markings; the flanks were dark brown with pale blue spots, and the anterior and posterior

surfaces of the thighs were uniform bright tomato red. A juvenile (UMMZ 121298), 18.6 mm. in snout-vent length, from the southeast slope of Volcán San Martín, Veracruz, México, had pale tan flanks lacking blue spots, but had red thighs. Apparently the ontogenetic changes in coloration proceed as follows: (1) flanks pale tan and thighs orange-yellow, both lacking spots, (2) flanks pale tan and thighs red, both lacking spots, (3) flanks dark brown with blue spots and thighs red, lacking spots, and (4) flanks and thighs dark brown, both having pale blue spots.

Natural History.—Smilisca cyanosticta inhabits humid tropical forest and cloud forest from the lowlands to elevations of about 1200 meters in Los Tuxtlas and to about 900 meters in northern Oaxaca. In these moist environments the frogs apparently are active throughout the year. Active individuals have been obtained in January, July, and August in Los Tuxtlas, Veracruz, in June and July in northern Oaxaca, in February and March at Chinajá, Guatemala, and Taylor and Smith reported (1945:589) activity in May at Piedras Negras, Guatemala. Calling males were observed as follows; in a rain barrel 11 kilometers north of Vista Hermosa, Oaxaca, México, on June 23-28, 1964; in a quiet pool in a stream 8 kilometers south of Yetla, Oaxaca, México, in July, 1963 (Dale L. Hoyt, personal communication); in and near springs flowing into a stream at Dos Amates, Veracruz, México, on August 4, 1959 (Douglas Robinson, personal communication); and in a water-filled depression in a log 10 kilometers west-northwest of Chinajá, Guatemala, on March 13, 1960. Taylor and Smith (1945:589) reported that individuals were found at night on the ground at the edge of temporary pools at Piedras Negras, Guatemala, on May 28-29, 1939. A clasping pair was found on a rock at the edge of a small stream on the south slope of Volcán San Martín, Veracruz, México, on July 11, 1959 (Douglas Robinson, personal communication).

Only one individual has been observed in a tree at night. In the daytime, individuals were found in elephant ear plants (*Xanthosoma*) at Chinajá, Guatemala.

The breeding call consists of one or two moderately short notes that are lower pitched than those of *S. baudini*, but higher pitched than those of *S. phaeota*. Each note has a duration of 0.25 to 0.45 seconds and is repeated at intervals of one-half minute to several minutes. Each note is a vibrant "waunk," having 110 to 180 pulses per second and dominant frequency of 1600 to 2100 cycles per second (Pl. 10B).

Apparently the eggs are deposited as loose clumps in the water. In eggs in the yolk plug stage of development, the diameter of the embryo is about 2.3 mm.; that of the outer envelope is 4.0 mm. Hatchling tadpoles have total lengths of 5.8 to 6.5 mm. and body lengths of 2.8 to 3.1 mm. The external gills are moderately long, slender, and filamentous; the yolk sac is still moderately large. The body and anterior part of the caudal musculature are dark brown; posteriorly the caudal musculature is pale brown. The caudal fins are creamy tan. The oral discs are large and ovoid. The growth of the tadpole is summarized in Table 10.

A typical tadpole in stage 30 of development (KU 87652 from 11 km. N Vista Hermosa, Oaxaca, México) can be described as follows:

Body length 9.5 mm.; tail length 15.5 mm.; total length 25.0 mm.; body slightly wider than deep; snout rounded laterally, broadly ovoid dorsally; eyes widely separated, directed dorsolaterally; nostril about midway between eye

and tip of snout; mouth anteroventral; spiracle sinistral, slightly posterior to midpoint of body and slightly below midline; anal tube dextral; caudal musculature slender, barely curved upward distally; dorsal fin not extending onto body, depth of dorsal fin slightly more than that of ventral fin on mid-length of tail; dorsal part of body dark brown; ventral surfaces transparent, lacking pigment; posterior edge of body pale cream-color; caudal musculature creamy white with interconnected brown spots; caudal fins transparent with small brown blotches on dorsal fin and posterior half of ventral fin; iris coppery bronze in life (Fig. 12). Mouth small, median part of upper lip bare; rest of mouth bordered by single row of bluntly rounded papillae; lateral fold present; tooth rows 2/3; all tooth-rows approximately equal in length; second upper row broadly interrupted medially; other rows complete; upper beak moderately deep, forming broad arch with slender lateral processes; lower beak slender, broadly V-shaped; both beaks finely serrate (Fig. 15C).

All tadpoles having fully developed mouth parts have 2/3 tooth rows. Little variation is noticeable in coloration. In many specimens the posterior edge of the body is dark brown instead of pale cream color. Mottling is rather dense on the caudal fins in all specimens; in some individuals pigment is concentrated along the anterior one-third of the lateral groove. In life the body is dark brown with greenish gold flecks ventrally; the caudal musculature is gray.

In each of two recently metamorphosed young the snout-vent length is 14.0 mm. Coloration of young in life (KU 87653 from 11 km. N Vista Hermosa, Oaxaca, México): "Dorsum pale tan with dark brown markings. Thighs orange-yellow; labial stripe white; iris bronze" (Duellman, field notes, July 10, 1964.)

Remarks.—Smith (1953:150) named *cyanosticta* as a subspecies of *Hyla phaeota*. The differences in cranial characters and certain external characters between *phaeota* and *cyanosticta* indicate that they are distinct species. Furthermore, a gap of about 350 kilometers exists between the known geographic ranges of the two kinds.

Distribution.—*Smilisca cyanostica* inhabits wet forests on the Atlantic slope of southern México and northern Central America from northern Oaxaca and southern Veracruz through northern Chiapas in México and into El Petén and northern Alta Verapaz in Guatemala (Fig. 2). Apparently the range is discontinuous, for in southern México the species is found in cloud forest at elevations of 830 to 900 meters on the northern slopes of the Sierra de Juárez. In the Sierra de Los Tuxtlas in southern Veracruz the species is found in wet forest at elevations of 300 to 1200 meters, but is absent in the intervening lowlands characterized by drier forest. In the west forests of northern Alta Verapaz and El Petén, Guatemala, the species is found at low elevations.

Specimens examined.—78, as follows: MEXICO: **Chiapas:** Monte Libano, MCZ 28271-9; 8 km. N San Fernando, 24 km. NE Tuxtla Gutierrez, UIMNH 41588. **Oaxaca:** 11 km. N Vista Hermosa, KU 84918-20 (skeletons), 87198-212, 87647 (eggs), 87648-52 (tadpoles), 87653 (young), UIMNH 57199-201; 8 km. S Yetla, KU 87213, UMMZ 124838 (8). **Veracruz:** Coyame, UMMZ 111459-60; between Coyame and Tebanco, UMMZ 121198; Dos Amates, UMMZ 121297; between Laguna de Catemaco and Volcán San Martín, UMMZ 121200; Volcán San Martín, UIMNH 35403-4, 35408-12, UMMZ 118163; SE slope Volcán San Martín, UMMZ 121199, 121295 (2), 121296, 121298.

GUATEMALA: **Alta Verapaz:** Chinajá, KU 55935-7, 55938 (skeleton). **El**

Petén: 10 km. NNW Chinajá (Alta Verapaz), KU 55934; Piedras Negras, CNHM 99006-7, 99227, UIMNH 28853, USNM 111139-41, 111143-7; 8 km. S Piedras Negras, CNHM 99008; Semicoch, USNM 35907.

Fig. 2. Map showing locality records for *Smilisca cyanosticta* (triangles) and *Smilisca phaeota* (circles).

Smilisca phaeota (Cope)

Hyla phaeota Cope, Proc. Acad. Nat. Sci. Philadelphia, 14 (9):358, 1862 [Holotype.—USNM 4347 from Turbo, Colombia; J. Cassin collector]. Boulenger, Catalogue Batrachia Salientia in British Museum, p. 402, Feb. 1, 1882. Werner, Sitzungsb. Akad. Wiss. München, 27:215, 1897. Günther, Biologia Centrali-Americana: Reptilia and Batrachia, p. 269, Sept. 1901. Nieden, Das Tierreich, Amphibia, Anura I, p. 261, June 1923. Dunn, Occas. Papers Boston Soc. Nat. Hist., 5:413, Oct. 10, 1931. Gaige, Hartweg, and Stuart, Occas. Papers Mus. Zool. Univ. Michigan, 357:4, Oct. 26, 1937. Cooper, Copeia, 2:122, June 30, 1944. Breder, Bull. Amer. Mus. Nat. Hist., 86(6):416, Aug. 26, 1946. Smith and Taylor, Bull. U. S. Natl. Mus., 194:88, June 17, 1948; Univ. Kansas Sci. Bull., 33:364, March 20, 1950. Taylor, Univ. Kansas Sci. Bull., 35(1):837, July 1, 1952. Brattstrom and Howell, Herpetologica, 10:117,

Aug. 1, 1954. Goin, Herpetologica, 14:120, July 23, 1958. Cochran, Bull. U. S. Natl. Mus., 220:57, 1961.

Hyla labialis Peters, Monats. Konigl. Akad. Wissen. Berlin, p. 463, 1863 [Holotype.—ZMB 4913 from "region of Bogotá," Colombia]; Monats. Konigl. Akad. Wissen. Berlin, p. 618, Oct. 16, 1873. Boulenger, Catalogue Batrachia and Salientia in British Museum, p. 397, Feb. 1, 1882.

Hyla baudini dolomedes Barbour, Occas. Papers Mus. Zool. Univ. Michigan, 129:11, Jan. 25, 1923 [Holotype.—MCZ 8539 from Río Esnápe, Sambú Valley, Darién, Panamá; Barbour and Brooks collectors]. Barbour and Loveridge, Bull. Mus. Comp. Zool. Harvard, 69:278, June, 1929.

Hyla phaeota phaeota, Smith, Herpetologica, 8:152, Jan. 30, 1953. Minton and Smith, Herpetologica, 16:103, June 17, 1960.

Smilisca phaeota, Starrett, Copeia, 4:303, Dec. 30, 1960.

Diagnosis.—Size large (♂ 65 mm., ♀ 78 mm.); skull as long as wide, lacking frontoparietal fontanelle; large supraorbital flanges having straight edges and extending posterolaterally; large squamosal not in contact with maxillary; tarsal fold moderately wide, full length of tarsus; inner metatarsal tubercle moderately large, low, flat, elliptical; hind limbs relatively long, tibia averaging more than 53 per cent of snout-vent length; labial stripe silvery white; lips lacking vertical bars; loreal region pale green; dark brown or black tympanic mark dispersing into brown venated pattern on flanks; posterior surfaces of thighs pale brown, with or without darker flecks or small cream-colored flecks. (Foregoing combination of characters distinguishing S. *phaeota* from any other species in genus.)

Description and Variation.—For the purposes of analyzing geographic variation in size and proportions, measurements were taken on ten adult males from each of five samples throughout the range of the species. Aside from the data summarized in Table 2, the average ratio of tibia length to snout-vent length is noticeably less in Colombian specimens (53.4 per cent, as compared with 54.8 to 57.8 per cent in the other samples) and the ratio of head length to

TABLE 2.—GEOGRAPHIC VARIATION IN SIZE AND PROPORTIONS IN MALES OF SMILISCA PHAEOTA. (MEANS IN PARENTHESES BELOW OBSERVED RANGES; DATA BASED OF TEN SPECIMENS FROM EACH LOCALITY.)

LOCALITY	Snout-vent length	Head width/ snout-vent length	Interorbital distance/ head width
Bonanza, Nicaragua.....	40.8–47.7 (43.7)	34.1–38.0 (36.3)	31.0–36.1 (35.4)
Heredia Prov., Costa Rica....	46.3–59.0 (51.7)	32.5–36.0 (35.0)	30.5–39.6 (34.7)
Puntarenas Prov., Costa Rica	53.6–64.9 (61.4)	32.6–36.1 (34.5)	31.0–38.0 (34.4)
Canal Zone, Panamá.....	52.4–65.5 (56.5)	33.5–37.6 (35.6)	31.3–37.2 (34.7)
Río Quesada, Colombia.....	52.6–61.0 (56.0)	33.1–37.1 (35.0)	30.1–33.9 (32.1)

snout-vent length is noticeably less in Costa Rican specimens (33.5 per cent as compared with 34.9 to 35.1 per cent in the other samples). Also, specimens from Heredia Province, Costa Rica, have a relatively smaller tympanum (62.7 to 80.4 [mean 68.4] per cent of the diameter of the eye, as compared with means of 74.0 to 77.9 per cent in the other samples).

Two populations are distinctive as regards the size of adult males. Specimens from the northern Caribbean lowlands of Nicaragua (Bonanza, the northernmost locality for the species) are remarkably small. Males having snout-vent lengths of between 40 and 43 mm. were breeding; the largest male found had a snout-vent length of 47.7 mm. The other extreme in size is attained in specimens from the Pacific lowlands of eastern Costa Rica and western Panamá, where most breeding males have snout-vent lengths of more than 55 mm.; the largest male had a snout-vent length of 64.9 mm.

The rather striking differences in size among certain samples and the minor differences in proportions among other samples show no geographic trends. Instead, the variations apparently are random among the samples. The data presented here possibly are the results of inadequate sampling, but more likely reflect actual differences in the populations.

The dorsal ground color of *Smilisca phaeota* is pale green to tan; the venter is creamy white. The dorsum is variously marked with dark olive-green or dark brown spots or blotches (Pl. 6C). A dark interorbital bar is usually present. Usually a large dark dorsal mark extends from the occiput to the sacral region, but in many individuals this blotch is replaced by two or three dark marks. The dorsal markings are irregular in shape and do not tend to form transverse bands or longitudinal bars. The hind limbs are marked by dark transverse bands, usually four or five on the thigh, five or six on the shank, and four on the tarsus. Two or three narrow bands are usually present on the proximal part of the fourth toe. The webbing on the feet is brown. The loreal region is pale green, bordered above by a narrow dark brown canthal stripe extending from the nostril to the orbit. The upper lip is silvery white. A broad dark brown or black mark extends posteriorly from the orbit, encompassing the tympanum, to a point above the insertion of the forelimb. The flanks are pale green or pale tan and marked with a fine dark brown or black venation. The anterior surfaces of the thighs usually are pale brown or grayish tan, sometimes having small, indistinct darker flecks. The posterior surfaces of the thighs are similarly colored, but in most specimens small but distinct dark flecks are present; in some specimens small cream-colored spots are also present on the posterior surfaces of the thighs. A distinct, narrow creamy-white anal stripe usually is present. A distinct white stripe is present on the outer edge of the tarsus and fifth toe; on the tarsus the white stripe is bordered below by dark brown. A white stripe also is present on the outer edge of the forearm and fourth finger. In breeding males the throat is dark gray.

Little geographic variation in color or pattern is evident. Few, if any, specimens from the Pacific lowlands of South America are green in life. (We have seen no living individuals from South America.) Some living individuals from Costa Rica and all those seen alive from Nicaragua have a tint of pale blue on the flanks. In some specimens the dorsal pattern is so faint as to be barely discernible, whereas in most specimens the pattern is bold.

The coloration in the living frogs is highly variable due to extreme metachrosis. Individuals of this species are capable of changing the dorsal colora-

tion from green to brown in a short period of time. Both green and brown individuals have been found active at night. Usually those individuals found hiding by day are brown. One individual from Finca La Sumbadora, Panamá (now KU 91914), was kept alive in the laboratory for nearly one month. This individual usually was pale green with tan dorsal markings at night and tan with pale green markings by day. On occasion the pale green dorsal markings were boldly outlined by bright dark green.

In living individuals from throughout the range of the species the iris is a bronze color, darkest medially with fine black reticulations.

Natural History.—Smilisca phaeota inhabits humid lowland tropical forest and seldom ascends the foothills to more than 1,000 meters. The rather equable climatic conditions, especially more or less evenly distributed rainfall throughout the year, permit this frog to be active most of the year. Dunn (1931:413) reported males calling on Barro Colorado Island, Panamá, in February and in July, and Breder (1946:416) noted calling individuals in the Chucanaque drainage of Darién, Panamá in January, March, July, August and October and in Costa Rica in April through August inclusively. Calling males were found at Bonanza, Nicaragua in March and in July.

At all times of year the usual daytime retreats for these frogs are near water; the frogs have been found in elephant ear plants (*Xanthosoma*) and in bromeliads; occasional individuals have been found sitting on shaded branches of bushes and trees. None has been observed on the ground or beneath groundcover by day.

The length of the breeding season cannot be determined definitely. The earliest date on which eggs have been found is May 23; Gaige, Hartweg, and Stuart (1937:5) reported a gravid female taken at El Recreo, Nicaragua, in September, and we have a gravid female taken at Almirante, Panamá, in March.

Males usually call from secluded spots at the edge of water. All calling males that we observed were on the ground within a few centimeters of the water. The males usually are hidden beneath an over-hanging leaf or some other cover; they definitely do not sit in the open like *Smilisca baudini*. Most calling males and clasping pairs have been found at the edges of small pools or shallow ditches, although occasional individuals are found at the edges of large ponds or streams.

The breeding call consists of one or two moderately short, low-pitched notes (duration 0.33 to 0.42 seconds), repeated at intervals of about 20 seconds to several minutes. Each note is a low, vibrant "wauk," having 100 to 130 pulses per second and a dominant frequency of 330 to 420 cycles per second (Pl. 10C).

The eggs are deposited in loose clumps amidst vegetation in the water. Hatchling tadpoles have total lengths of 8.7 to 10.6 mm., and body lengths of 4.1 to 4.5 mm. The external gills are long and filamentous, and the yolk sac is large. The head and caudal musculature are dark brownish black, and the caudal fins are gray. The oral discs are large and roughly circular. The growth and development of the tadpoles are summarized in table 11 and figure 16.

A typical tadpole in stage 30 of development (KU 68482 from the Río Chitaría, Cartago Province, Costa Rica) may be described as follows: body length 9.7 mm.; tail length 14.6 mm.; total length 24.3 mm.; body as wide as deep; snout rounded dorsally and laterally; eyes widely separated, directed

dorsolaterally; nostril about midway between eye and tip of snout; mouth anteroventral; spiracle sinistral, about midway on length of body and slightly below midline; anal tube dextral; caudal musculature slender, curved upward distally; dorsal fin extending onto body; depth of dorsal fin slightly less than that of ventral fin at mid-length of tail; dorsal part of body pale brown; ventral surfaces transparent with scattered pigment; pale cream-colored, crescent-shaped mark on posterior edge of body; caudal musculature pale creamy tan with scattered pale brown spots; caudal fins transparent with scattered small brown blotches on dorsal and ventral fins; iris pale bronze in life (Fig. 13); mouth small; median part of upper lip bare; rest of mouth bordered by one row of pointed papillae; lateral fold present; tooth-rows 2/3, first upper row longest; second upper row slightly shorter, broadly interrupted medially; three lower rows complete, equal in length, slightly shorter than second upper row; upper beak moderately deep, forming broad arch with slender lateral processes; lower beak slender, broadly V-shaped; both beaks serrate (Fig. 15E).

In tadpoles having fully developed mouth-parts the tooth-row formula of 2/3 is invariable. The pale crescent-shaped mark on the posterior part of the body curves anterodorsally on the dorsal surface of the body. These marks in dorsal view give the appearance of a pair of short, pale stripes on the posterior part of the body. Most specimens from Costa Rica have the pale coloration like that described above, but some individuals (notable KU 87683 from Guápiles, Costa Rica, KU 87707 from Finca Tepeyac, Nicaragua, and KU 87708 from Bonanza, Nicaragua) have much more pigment. In these specimens the same color pattern obtains as in the pallid individuals, but the pigmentation is dense. This is especially noticeable on the tail.

Recently metamorphosed young have snout-vent lengths of 12.7 to 16.7 mm. (average, 14.3 mm. in eleven specimens). Coloration of young in life (KU 68484 from Río Chitaría, Cartago Province, Costa Rica): "Dorsum pale tan; side of head and flanks darker brown, separated from tan dorsum by an indistinct cream stripe. Limbs pale yellow; thighs flecked with brown; shank and tarsus yellowish tan with indistinct brown bars. Soles of feet brown. Belly white; throat dusty cream flecked with silvery white. Upper lip silvery white. Iris bright gold with black flecks. Heels, tarsal and anal stripes white" (Duellman, field notes, May 23, 1961).

Remarks.—Peters (1863:463) named *Hyla labialis* from the "region of Bogotá, Colombia", but in 1873 regarded his new species as identical with *Hyla phaeota* Cope, 1862, from Turbo, Colombia. The name *Hyla labialis* has been used for frogs from the northern Andes in Colombia (see Dunn, 1944:72, and Stebbins and Hendrickson, 1959:522, for discussion of nomenclature). Rivero (1961:131) used the name *Hyla vilsoniana* Cope, 1899, for the frogs from the northern Andes previously referred to *Hyla labialis*. A review of the nomenclature and taxonomy of these frogs, which superficially resemble *Smilisca* but are unrelated, is beyond the scope of the present study.

Hyla baudini dolomedes Barbour, 1923, is based on a small *Smilisca phaeota* (MCZ 8539) having a snout-vent length of 45.5 mm. Dunn (1931a:413) placed *dolomedes* in the synonymy of *Smilisca phaeota*. We have examined the holotype of *dolomedes* and agree with Dunn's assignment.

Smith (1953:150) described *Hyla phaeota cyanosticta* from Guatemala. Our studies on the external morphology, coloration, and especially the cranial osteology provide evidence that *cyanosticta* is a species distinct from *phaeota*.

Distribution.—*Smilisca phaeota* inhabits humid tropical forests from northeastern Nicaragua southward on the Caribbean lowlands to elevations of about 1000 meters and on the Pacific lowlands of Costa Rica, exclusive of the arid regions of Guanacaste, throughout the lowlands of Panamá, exclusive of the savannas of the Pacific lowland and the Azuero Peninsula, and southward on the Pacific slopes of South America through Colombia to west-central Ecuador; also the valleys of the Río Cauca and Río Magdalena in Colombia (Fig. 2).

Specimens examined.—528, as follows: NICARAGUA: **Matagalapa:** Finca Tepeyac, 10 km. N, 9 km. E Matagalpa, KU 85439, 87707 (tadpoles); Matagalpa, MCZ 3546-7, UMMZ 92367; 19 km. N Matagalpa, UMMZ 116495-6. **Zelaya:** Bonanza, KU 84854-62, 84950-2 (skeletons), 85440-50, 87708-9 (tadpoles); Cukra, AMNH 80618; Río Mico, 16 km. E Recreo, UMMZ 79711 (6), 79712 (4); junction Río Mico and Río Siguia, UMMZ 79713 (10); Río Siguia, 11 km. NW Rama, UMMZ 79714 (14), 79715 (11), 79716 (21), 79717, 79718 (3).

COSTA RICA: **Alajuela:** Cinchona, KU 32255, 64286-8; 5 km. S Ciudad Quesada, USC 8077; Laguna Monte Alegre, KU 64289-90; Las Playuelas, 11 km. S Los Chiles, USC 7216; San Carlos, USNM 29961.

Cartago: Moravia de Turrialba, KU 32212-47, 37133-5, 41093 (skeleton), 64280-1, USC 7243 (3); Peralta, KU 32271-2; Río Chitaría, 3 km. NNE Pavones, KU 64273-9, 68477 (eggs), 68478-83 (tadpoles), 68484 (young); Río Reventazón, MCZ 29196-203, UMMZ 117677 (9); Turrialba, KU 25720-2, 32209-11, 32266-8, 32273-4, 37136-67, 41090-2 (skeletons), 64270-2, MCZ 29221, 29222 (tadpoles), 29269-70, USNM 29934.

Guanacaste: Tilarán, KU 36805-7; 8 km. NE Tilarán, KU 36803-4.

Heredia: Barranca del Río Sarapiquí below Isla Bonita, KU 64282-3; Cariblanco, KU 32256-60, 41094 (skeleton), 64284, MCZ 7967; Isla Bonita, KU 32250-4; 4.2 km. W Puerto Viejo, KU 64285, 68485; 7.5 km. W Puerto Viejo, KU 68486; 1 km. S Puerto Viejo, KU 86518.

Limón: Bambú, USC 7182 (4); Batán, UMMZ 118582; Coén, MCZ 9825; La Lola, KU 32262-4, UF 4029, UMMZ 117678 (3); Los Diamantes, CNHM 101295-8, KU 25723-4, 32265, 64267-9; Pandora, UMMZ 122650 (2), USC 7188 (3), 7190; Puerto Limón, KU 32261; Río Larí at Río Dipari, 21 km. SW Amubre, USC 7177; Río Toro Amarillo, 7 km. W Guápiles, KU 86519, 87683 (tadpoles); Suretka, KU 36808-10, 37168.

Puntarenas: Agua Buena, KU 36790; 1.6 km. E Buenos Aires, UMMZ 117578; 3 km. NW Buenos Aires, KU 64304; 4 km. N, 15 km. W Dominical, KU 68491-2 (tadpoles); Esparta, MCZ 8029-30, 8032; Golfito, KU 32270; 6 km. E Golfito, KU 84999-500 (skeletons); Gromaco, UMMZ 123677 (4); Palmar, KU 32269; 4 km. ESE Palmar Sur, KU 64305-6; 5.6 km. SE Palmar Sur, KU 68489 (tadpoles); 7.0 km. SE Palmar Sur, KU 68490 (young); 8.5 km. SE Piedras Blancas, KU 64292-303; Quebrada Boruca, 22 km. E Palmar Norte, KU 64291; Rincón, "Camp Seattle," Peninsula de Osa, UMMZ 123676 (3), USC 7254; Río Ferruviosa, 7 km. S Rincón, USC 7235; 1.6 km. WNW Villa Neily, KU 68493 (young), 68494 (tadpoles).

San José: San Isidro el General, KU 32249, UMMZ 75025; 10 km. N San Isidro el General, MCZ 29099-103; 13 km. WSW San Isidro el General, KU 86517; 15 km. WSW San Isidro el General, KU 68487 (tadpoles), 68488 (young), 68495 (young); 20 km. WSW San Isidro el General, KU 32248.

PANAMA: No province: Cano Saddle, USNM 69588; Punta de Pena, USNM 38733; Quipo, AMNH 18925-6. **Bocas del Toro:** Almirante, KU 80080, 91835-6; 1.6 km. W Almirante, KU 91837; 3 km. W Almirante, KU 91824 (skeleton), 91838-43, 91906-7; 11 km. NW Almirante, CNHM 67853-61; 13 km. W Almirante, KU 91825-7 (skeletons), 91844-9; Fish Creek, KU 92329; Isla Popa, KU 91850-1. **Canal Zone:** Barro Colorado Island, CNHM 6007, 13316, 13325, 13331, 13360-2, 13377-8, MCZ 24191-5, UF 7523, UMMZ 63547-60, 64457, 69497 (3); 3.7 km. W Cocoli, KU 67916; Fort Sherman, MCZ 10139; Gatun, MCZ 35644; Junction roads C25B and C16, TNHC 23839;

Madden Forest Preserve, TNHC 23837-8. **Coclé:** El Valle, KU 77521-4, 77649 (tadpole), TNHC 23369. **Comarca del Barú:** Progreso, UMMZ 61085-9. **Colón:** Achiote, KU 77516-20, 77648 (young); Río Candelaria, CNHM 67-851-2. **Darién:** Río Esnápe, Sambú Valley, MCZ 8539; Río Sucubti, Chalichiman's Creek, AMNH 40512; Camp Creek, AMNH 40758-9; Camp Creek, Camp Townsend, AMNH 40988. **Panamá:** NW slope Cerro Prominente, KU 80459; Finca La Sumbadora, KU 91914 (skeleton). **Chiriquí:** 2 km. W Concepción, AMNH 68910.

Colombia: **Antioquia:** Puerto Berrio, CNHM 30805 (Goin); Turbo, USNM 39899. **Caldas:** Pueblorrica, Santa Cecilia, CNHM 54768-71 (Goin). **Choco:** No specific locality, AMNH 3984-6; Andagoya, BMNH 1915. 10. 21. 69-70, CNHM 81857 (Goin); Golfo de Urabá, CNHM 63881 (Goin); Peña Lisa, Condoto, BMNH 1913. 11. 12. 118-125, 1913. 11. 12. 137-146 (Goin); Pizarro, CNHM 4451-3, 4455-61 (Goin); Río San Juan, Playa del Oro, CNHM 54772 (Goin); Río Quesada, AMNH 13615-77; 37 km. up Río Puné, AMNH 13688; 48 km. up Río Puné, AMNH 13689. **Narino:** Tumaco, Río Rosario, CJG 2310-13 (Goin). **Valle:** Buenaventura, BMNH 1895. 11. 16. 82 (Goin); Raposa, WAT 166, 346-47, 388 (Goin); Río Calima above Córdoba, CJG 2249-57 (Goin).

Ecuador: No province: Bulun, AMNH 10620. **Esmeraldas:** Cachabé, AMNH 10625-8; Río Capayas, CNHM 35712; Río Sapaya, UMMZ 58910 (5); Salidero, AMNH 10623-4; San Javier, AMNH 10618. **Guayas:** Hacienda Balao Chico, UMMZ 123904. **Imbabura:** Pambelar, AMNH 10629, 10631. **Pichincha:** Hacienda Espinosa, 9 km. W Santo Domingo de los Colorados, KU 40220.

Smilisca puma (Cope), new combination

Hyla puma Cope, Proc. Amer. Philos. Soc., 22:183, 1885 [Holotype.—USNM 13735 from Nicaragua; J. F. Moser collector]. Günther, Biologia Centrali-Americana: Reptilia and Batrachia, p. 270, Sept., 1901. Nieden, Das Tierreich, Amphibia, Anura I, p. 251, June, 1923. Cochran, Bull. U. S. Natl. Mus., 220:58, 1961.

Hyla wellmanorum Taylor, Univ. Kansas Sci. Bull. 25(1):843, July 1, 1952 [Holotype.—KU 30302 from Batán, Limón, Costa Rica, Edward H. Taylor collector]; Univ. Kansas Sci. Bull., 36(1):626, June 1, 1954. Duellman and Berg, Univ. Kansas Publ. Mus. Nat. Hist., 15:194, Oct. 26, 1962.

Smilisca wellmanorum, Starrett, Copeia, 4:303, Dec. 30, 1960.

Diagnosis.—Size small (♂ 38.0 mm., ♀ 46.0 mm.), differing from other species in the genus by the following combination of characters: skull about as long as broad; frontoparietal fontanelle keyhole-shaped; supraorbital flanges absent; squamosal small, not in contact with maxillary; bony portion of ethmoid terminating at anterior edge of orbit; tarsal fold weak, two-thirds length of tarsus; inner metatarsal tubercle small, low, flat, elliptical; snout rounded in dorsal profile; lips thin and flaring; fingers having only vestige of web; toes one-half webbed; diameter of tympanum about two-thirds that of eye; narrow labial stripe white; pair of dark brown (sometimes interconnected) stripes on tan dorsum; no blue spots on flanks or thighs; vocal sac in breeding males pale brown. (Foregoing combination of characters distinguishing S. *puma* from other species in genus.)

Description and variation.—Ten breeding males from the vicinity of Puerto Viejo, Heredia Province, Costa Rica, have snout-vent lengths of 32.5 to 37.9 mm. (34.8 mm.). In these specimens, the length of the tibia to the snout-vent length is 0.48 to 0.53 (0.51), and the tympanum/eye ratio is 0.52 to 0.72 (0.65). Seven females have snout-vent lengths of 40.8 to 45.8 mm. (43.9 mm.).

No individual has more than a vestige of a web between the second and third and fourth fingers. None has a web between the first and second fingers. Breeding males lack nuptial excrescences on the thumbs. The vocal sac is moderately large and bilobed.

In preserved specimens the dorsal ground color varies from yellowish tan to grayish brown. All specimens have dark brown dorsal markings in the form of a pair of dorsal stripes, variously modified (Pl. 7A). In some specimens, such as KU 91716, the stripes are discrete and extend from the postorbital region nearly to the vent. In most specimens the stripes are connected by a transverse mark in the scapular region and in many others also by a transverse mark in the sacral region. In some specimens the stripes are fragmented posteriorly; fragmentation is extreme in KU 30300, in which the dorsal pattern consists of two series of dark longitudinal dashes. The other extreme is a nearly complete fusion of the stripes, as in KU 91714. A dark brown interorbital bar usually extends onto the eyelids, but in some specimens this is reduced to a short V-shaped mark or small spot between the eyes. There is no dark post-tympanic mark, but dark brown pigment forms a venated pattern from the axilla to the mid-flank; the inguinal region is white, finely mottled with dark brown. The dorsal surfaces of the hind limbs are colored like the body and have two or three dark brown transverse marks on the thighs, three to five marks on the shanks, and one or two marks or irregularly arranged dark flecks on the tarsi. The anterior and posterior surfaces of the thighs are pale tan to brown. The webbing of the feet is tan to grayish brown. A narrow white labial stripe, white anal stripe, and narrow white stripes on the tarsi and outer edges of the forelimbs are invariably present. The ventral surfaces are creamy white.

In life the dorsum is tan or pale brown with dark brown markings. Some individuals have scattered metallic green flecks on the dorsum. The flanks are mottled dark brown and creamy white. The posterior surfaces of the thighs are dark brown. The vocal sacs are grayish brown, and the iris is a deep bronze color.

Natural History.—Smilisca puma inhabits humid lowland tropical forests having more or less evenly distributed rainfall throughout the year. The equable climatic conditions seemingly permit these frogs to be active throughout most of the year. Taylor (1952:846) found calling males at Batán, Costa Rica, on July 20, 1951. We found the species breeding near Puerto Viejo, Costa Rica, on February 19, June 18, July 13, and July 31. Specimens of calling males from Costa Rica in the collection at the University of Southern California were obtained in February at La Fortuna, on August 22 at Los Diamantes, on August 30 at Jabillos, and on September 5 at La Lola. Gravid females were collected in June, July and August.

Males call from shallow water. All breeding congregations of this species that we have found were in a grassy marsh, 7.5 kilometers west of Puerto Viejo, Costa Rica. Tadpoles were found in water-filled depressions in the marsh at night. When first observed, tadpoles were near the surface of the water; they responded to light by quickly taking refuge in the dense grass. No tadpoles were observed by day.

The breeding call consists of a low squawk, usually followed by a series of one or more rattling secondary notes (duration of primary notes, 0.06-0.35

seconds; of secondary notes, 0.10 to 0.47 seconds), repeated at intervals of 5 to 55 seconds. The primary notes have 187 to 240 pulses per second and major frequencies of about 740 to 1870 cycles per second (Pl. 11A).

Only six tadpoles are available for study. Four of them in stage 34 of development have body lengths of 9.0 to 9.5 mm., tail lengths of 14.0 to 15.0 mm., and total lengths of 23.0 to 24.5 mm. One tadpole in stage 38 and one in stage 40 have total lengths of 31.0 mm. A typical tadpole in stage 34 of development (KU 91807 from 7.5 km. W Puerto Viejo, Heredia Province, Costa Rica) has a body length of 9.5 mm., tail length of 15.0 mm., and total length of 24.5 mm.; body about three-fourths as deep as wide; snout rounded dorsally and laterally; eyes widely separated, directed dorsolaterally; nostril about midway between eye and tip of snout; mouth anteroventral; spiracle sinistral, about two-thirds distance from snout to posterior end of body and slightly below midline; anal tube dextral; caudal musculature slender, barely curved upward distally; dorsal fin extending onto body; at mid-length of tail, depth of caudal musculature equal to that of dorsal fin and ventral fin; body grayish brown, palest ventrally; caudal musculature pale creamy yellow with bold gray reticulations; caudal fins transparent with gray reticulations anteriorly and black flecks posteriorly on both fins (Fig. 14A). Median part of upper lip bare; rest of mouth bordered by two rows of short blunt papillae; lateral fold present; tooth-rows 2/3; upper rows equal in length; second upper row broadly interrupted medially; three lower rows complete, first and second rows equal in length, slightly shorter than upper rows; third lower row noticeably shorter; upper beak shallow, forming broad, continuous arch with slender lateral processes; lower beak slender, broadly V-shaped, both beaks finely serrate (Fig. 15B).

All six tadpoles are colored alike, except that in the larger specimens scattered white flecks are present on the ventral surface of the body, and the dark reticulations continue farther posteriorly on the caudal fins than in the smaller tadpoles. In two specimens the third lower tooth-row is only about one-half the length of the other lower rows, and in one specimen the second lower tooth-row is shorter than the first. Coloration of tadpoles in life: "Body olive-brown with silvery green flecks laterally. Caudal musculature olive-brown with greenish tan flecks. Fins brown with greenish gold flecks. Iris deep bronze." (Duellman, field notes, February 19, 1965).

One recently metamorphosed young (KU 91808) has a snout-vent length of 12.4 mm. In life this frog had a pale tan dorsum with dark brown markings, yellowish tan posterior surfaces of thighs, grayish brown throat, and bronze iris.

Remarks.—The identity of Cope's *Hyla puma* has not been known. The name has appeared in various compilations, but no workers have referred any of their specimens to that species. Examination of the holotype (USNM 13735), an adult female, revealed the presence of the following combination of characters: snout-vent length 45.8 mm., snout blunt above and rounded laterally, nostrils close to tip of snout, lips thin and flaring, a vestige of a web on the hands, feet about one-half webbed, tarsal fold weak and extending about two-thirds length of tarsus, dorsal markings consisting of a faded dark interorbital bar and a pair of faded longitudinal brown marks connected by a transverse band in the scapular region. The type agrees well with specimens of *Smilisca wellmanorum* (Taylor, 1952); the vestigial webbing on the

hands and the dorsal coloration are especially significant. Consequently, we consider *Hyla wellmanorum* Taylor, 1952, to be a synonym of *Hyla puma* Cope, 1885. Cope gave only "Nicaragua" as the locality for *Hyla puma*. The specimen was part of a collection received at the United States National Museum from Lt. J. F. Moser. Among the species in the collection are *Dentrobates pumilio, Phyllomedusa helenae, Corythophanes cristatus, Pliocercus dimidatus, Tretanorhinus nigroluteus,* and others characteristically found on the Caribbean lowlands of Central America. Thus, it seems reasonable to assume that the type specimen of *Hyla puma* came from the Caribbean lowlands. Though no other Nicaraguan specimens have been found by us, numerous specimens are known from the Caribbean lowlands of Costa Rica.

Cochran (1961:58), in her catalogue of type specimens in the United States National Museum, listed *Hyla puma* Cope, 1885, as a synonym of *Hyla molitor* Schmidt, 1857. She made no qualifying statements. Schmidt (1858: 246), in his descriptions of the species in the year following his publication of the names and Latin diagnoses, stated: "Dorsum uniformly gray, more intensive on back, fading away laterally and on extremities; in every-day-life this blue would be called *Mueller's Blau*. A delicately dotted black line runs on the canthus rostralis from the opening of the nose to the corner of the eye. In the armpits, on the flanks and the thighs two of our three specimens have black marblings." [Free translation] Certainly on the basis of coloration *Hyla puma* is distinctly different from *Hyla molitor*.

Distribution.—This species lives in the wet, forested regions of the Caribbean lowlands of Costa Rica and presumably southern Nicaragua (Fig. 3). All specimens are from low elevations; the highest known elevation for the occurrence of this frog is 285 meters at Laguna Bonilla.

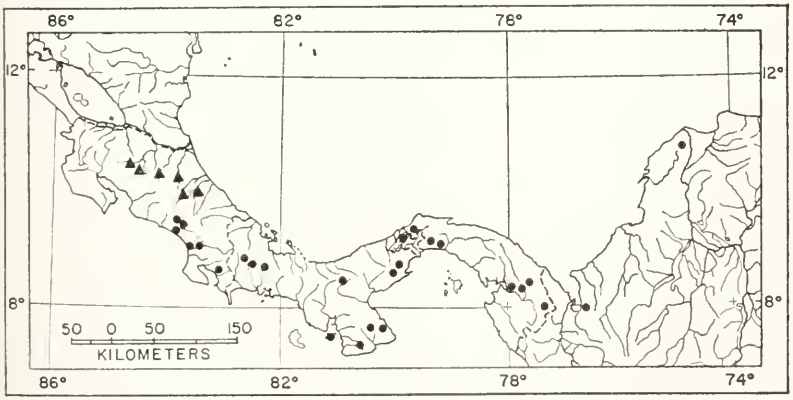


FIG. 3. Map showing locality records for *Smilisca puma* (triangles) and *Smilisca sila* (circles).

Specimens examined.—62, as follows: NICARAGUA: No specific locality, USNM 13735.

COSTA RICA: **Alajuela:** Jabillos, 5 km. N Santa Clara, USC 8058 (6); 5 km. W La Fortuna, USC 8078 (2); Río La Fortuna at La Fortuna, USC 7151 (3). **Cartago:** Laguna Bonilla, tunnel camp near Peralta, KU 32171. **Heredia:** Puerto Viejo, KU 86521; 5.9 km. W Puerto Viejo, KU 64307; 7.5 km. W Puerto

Viejo, KU 64308-10, 64311 (skeleton), 64312-15, 68635-6 (skeletons), 85001-2 (skeletons), 86520, 87770-1 (skeletons), 91709-16, 91791-2, 91807 (tadpoles), 91808 (young). **Limon:** Batán, KU 30300-2; La Lola, KU 32169, USC 141, 201, 8067; Los Diamantes, KU 32170, UMMZ 118470 (6), USC 212; 2.4 km. E Los Diamantes, USC 8049 (5).

Smilisca sila new species

Hyla gabbi, Noble, Proc. Biol. Soc. Washington, 37:66, Feb. 21, 1924. Dunn, Occas. Papers Boston Soc. Nat. Hist., 5:413, Oct. 10, 1931. Schmidt, Smithsonian Misc. Coll., 89(1):6, March 16, 1933.

Hyla sordida, Dunn, Copeia, 3:166, Nov. 19, 1937. Cooper, Copeia, 2:121, June 30, 1944. Breder, Bull. Amer. Mus. Nat. Hist., 86(8):417, Aug. 26, 1946.

Hyla phaeota, Breder, Bull. Amer. Mus. Nat. Hist., 86(8): pl. 55, Aug. 26, 1946.

Holotype.—Adult male, KU 91852 from a small stream at the north edge of the village of El Volcán, Chiriquí Province, Panamá, elevation 1280 meters; obtained on Feb. 5, 1965, by William E. Duellman.

Paratypes.—KU 91853-74, collected with the holotype.

Diagnosis.—Size moderate (♂ 45.0 mm., ♀ 62.2 mm.); skull wider than long, having large, ovoid frontoparietal fontanelle; supraorbital flanges absent; squamosal small, not contacting maxillary; bony section of ethmoid extending anteriorly between nasals; tarsal fold weak, full length of tarsus; inner metatarsal tubercle low, flat, elliptical; lips thick, rounded, not flaring; fingers one-third webbed; toes three-fourths webbed; diameter of tympanum about one-half that of eye; margin of upper lip faintly marked by interrupted creamy white stripe; dark spots on dorsum; pale flecks on flanks and posterior surfaces of thighs; vocal sacs in breeding males dark brown. (Foregoing combination of characters distinguishing *S. sila* from any other species in genus.)

Description of holotype.—Snout-vent length 36.6 mm.; tibia length 19.8 mm., 54.1 per cent of snout-vent length; foot length 15.5 mm., 42.3 per cent of snout-vent length; head length 12.7 mm., 34.7 per cent of snout-vent length; head width 13.3 mm., 36.8 per cent of snout-vent length; snout short, in lateral profile truncate, only slightly rounded above, in dorsal profile rounded; canthus rounded; loreal region noticeably concave; lips thick, rounded, not flaring; nostrils not protuberant, directed laterally; internarial distance 3.0 mm.; internarial area flat; top of head flat; interorbital distance 3.5 mm., 26.3 per cent of head width; diameter of eye 4.2 mm., thrice distance (1.4 mm.) from tympanum to eye, and half again distance (2.8 mm.) from orbit to nostril; pupil horizontally ovoid; width of eyelid 2.8 mm., 21.1 per cent of head width; dermal fold from posterior corner of orbit covering upper edge of tympanum to point above insertion of forelimb; diameter of tympanum 2.3 mm., 54.7 per cent of diameter of eye; no axillary membrane; arms moderately robust; weak fold on wrist; faintly scalloped fold along ventrolateral margin of forearm; fingers short, slender; fingers from shortest to longest, 1-2-4-3; vestige of web between first and second fingers; others about two-fifths webbed; discs moderate, diameter of that on third finger about one-third diameter of eye; triangular outer palmar tubercle; elliptical inner palmar tubercle on base of pollex; subarticular tubercles large, conical, none bifid; supernumerary tubercles few, large, conical; brown nuptial excrescence on prepollex; heels overlap by about one-fifth length of shank when hind limbs adpressed; tibiotarsal articulation extending to nostril; tarsal fold weak, extending nearly full length of tarsus; inner metatarsal tubercle elliptical, flat; outer metatarsal tubercle absent; toes moderately long; toes from shortest to longest, 1-2-3-5-4, third and fifth about equal in length; discs about same size as those on fingers; webbing

extending to middle of penultimate phalanx on all toes, except only to distal end of antepenultimate phalanx of fourth toe; subarticular tubercles round; supernumerary tubercles large, round, present only on proximal digits. Anal opening directed posteriorly at level of upper edge of thighs; no noticeable anal sheath; flat tubercles ventrolateral to anal opening large; skin of chest, belly, and posterior surfaces of thighs granular; other surfaces smooth; tongue broadly cordiform, shallowly notched posteriorly, and barely free behind; vomerine teeth 4-4, situated on ventral surfaces of separated rounded prominences between posterior margins of small, ovoid inner nares; vocal slits long, each situated along inner margin of ramus; color (in preservative) pinkish tan above with irregular olive-brown markings forming interconnected spots on back; four bars on dorsal surface of each thigh; five bars on shank, and three on tarsus; inguinal region white with black mottling; posterior surfaces of thighs yellowish tan proximally, dark brown distally; margins of lips grayish white with brown markings; ventral surfaces of hands and feet grayish brown; belly and posterior part of throat creamy white; anterior part of throat brown.

Description and variation.—Ten breeding males from Finca La Sumbadora, Panamá, have snout-vent lengths of 40.0 to 44.8 mm. (42.3 mm.). In these specimens the tibia/snout-vent length ratio is 0.50 to 0.57 (0.54), and the tympanum/eye ratio is 0.48 to 0.58 (0.53). There is a geographic gradient in size; specimens from the western part of the range (southern Costa Rica) are smaller than those from the eastern part of the range (eastern Panamá). Five males from the Pacific lowlands of southern Costa Rica have snout-vent lengths of 31.6 to 38.2 mm. (34.7 mm.); ten males from El Volcán, Chiriquí, Panamá, 32.6 to 37.9 mm. (36.4 mm.), and eight males from Barro Colorado Island, Canal Zone, 38.2 to 42.0 mm. (35.6 mm.). These are smaller than the males from Finca La Sumbadora, which is east of the Canal Zone. Ten females from El Volcán have snout-vent lengths of 44.2 to 55.6 mm. (49.2 mm.), as compared 56.1 to 62.2 mm. (58.2 mm.) in three females from Finca La Sumbadora.

Large females have scattered small tubercles on the head and back; tubercles occur in males from Costa Rica and in some males from western Panamá. The truncate snout is characteristic of both sexes.

The coloration of *Smilisca sila* consists of a gray, tan, or pale reddish brown dorsal ground color and a creamy white venter. The dorsum is marked by dark brown, olive-brown, or dark reddish brown spots or blotches (Pl. 7B). Usually the blotches are discrete, but in some individuals they are interconnected and form an irregular dark mark on the dorsum. There is no tendency for the blotches to form transverse bars as in *Smilisca sordida*. In one specimen (KU 80467) the blotches are fused and form two wide irregular longitudinal stripes, as in *Smilisca puma*. In some females the dorsal markings are reduced to a few small spots or are nearly absent (KU 92332), whereas in other females the dorsal markings are bold. In one female (KU 91894) the dorsal markings are narrowly bordered by pale blue, and numerous pale blue flecks are present on the pale brown dorsum. In many individuals of both sexes small white flecks are present on the dorsal surfaces.

Usually the flanks and posterior surfaces of the thighs have black mottling enclosing pale blue spots and flecks, respectively. The dorsal surfaces of the limbs are marked by dark brown transverse bars; usually three or four bars are present on each forearm, thigh, and shank. The coloration of the flanks and limbs varies geographically. Specimens from southern Costa Rica and western Panamá have distinct bars on the limbs; the posterior surfaces of the thighs have brown reticulations enclosing small blue flecks in specimens from

Costa Rica and bolder, black reticulations enclosing large pale blue spots in specimens from western Panamá. In specimens from Costa Rica the flanks are brown with pale blue flecks, whereas in those from Chiriquí, Panamá, the flanks are pale blue with dark brown mottling in the inguinal region. Frogs from El Valle and Cerro la Campana usually have distinct bars on the limbs; the posterior surfaces of the thighs are colored as in frogs from Chiriquí, and the inguinal region is pale blue with coarse brown mottling. Specimens from Barro Colorado Island are marked like those from El Valle and Cerro la Campana, except that on the posterior surfaces of the thighs fine black reticulations enclose many dark blue spots. In specimens from Darién and from Panamá Province east of the Canal Zone (Altos de Pacora, Cerro Jefe, Finca La Sumbadora, and Río Pacora), the markings on the dorsal surfaces of the limbs are indistinct or absent in males, but distinct in some females. Intense brown and black pigment forms fine reticulations delimiting bold blue spots on the flanks; this coloration extends to the axilla in many specimens. Fine black reticulations enclose many dark blue spots on the posterior surfaces of the thighs.

In females, the throat is creamy white; in some specimens scattered brown flecks are present on the chin and throat. In breeding males the anterior part of the throat is dark gray or dark brown.

The coloration in life is as variable as it is in preservative. In life the holotype had a tan dorsum with dark olive-green irregular markings and small green flecks. The limbs were tan with dark brown transverse bars. The flanks were grayish tan anteriorly; the inguinal region and posterior surfaces of thighs were blue with black mottling. The belly was creamy white, and the throat was brown with creamy yellow flecks. The iris was a dull bronze color. Among the paratypes, some individuals had green flecks, others did not. The inguinal region and posterior surfaces of the thighs were pale blue, pale yellowish green, or grayish tan with black mottling. The blue was most noticeable in females.

Colors of a male from Finca La Sumbadora, Panamá, were described as follows: "Dorsum olive-brown; irregular dark brown blotches, pale green flecks, and raised creamy yellow spots on dorsal surfaces; belly creamy white; throat grayish brown; undersides of limbs grayish tan; groin, anterior and posterior surface of thigh, inner surface of shank, anterior edge of tarsus, and proximal parts of third and fourth toes pale blue marbled with dark brown and black; webbing brown; iris pale bronze, finely reticulated with black." (Duellman, field notes, January 28, 1964.)

A female (now KU 91894) from Altos de Pacora, Panamá, was described as follows: "An irregular dark brown, green-bordered figure on head and back; dark brown, green-bordered bands on limbs—all on a lighter brown and heavily green-spotted background. These markings are more vivid at night than during the day. Lower sides, from midbody onto front of thighs and rear of thighs onto venter of shanks to heels and thence dorsally onto basal portions of toes heavily blue spotted on a light brown (front of thighs and venter of shanks) to blackish brown background. Venter cream. Iris gray-brown, finely veined with dark brown." (Charles W. Myers, field notes, December 14, 1964.) Note that in the earlier discussion of coloration of preserved specimens, the green spots and borders have changed to pale blue after six months in alcohol.

In living individuals from Costa Rica and Panamá west of the Canal Zone, the blue coloration on the flanks and thighs is much less conspicuous than in specimens from eastern Panamá. The color of the iris is variable, even in frogs from one locality. The coloration of the iris in 13 living frogs (now KU 92333-45) from Valle Hornito, Chiriquí, Panamá, was described as follows: "Iris variable—from pale to dark brown; in a few the iris has a golden cast to the brown; in a few others the lower half of the iris is pale gray with the upper half being light brown." (Charles W. Myers, field notes, April 24, 1965).

Natural history.—Smilisca sila inhabits the Pacific slopes of lower Central America where a pronounced dry season occurs. We have records of males calling in December through May and also in August (latter date from El Volcán, Chiriquí, Panamá). The breeding season seems to be correlated with the time of the year when the water is clear and at a low level in the streams where these frogs breed.

Males call from the edges of small, shallow streams, from rocks in the streams, or less frequently from vegetation overhanging the streams. Females are most frequently found on the banks of streams, and clasping pairs usually are in shallow pools in streams. One individual was found in a bromeliad about three meters above the ground in the daytime.

The breeding call consists of a low squawk, usually followed by a series of one or more rattling secondary notes (duration of primary notes, 0.06 to 0.28 seconds; of secondary notes, 0.14 to 0.48 seconds), repeated at intervals of 4 to 20 seconds. The primary notes have 97 to 120 pulses per second and major frequencies of about 900 to 2220 cycles per second (Pl. 11B).

Eggs were obtained artificially in the field; the average length of ten embryos in the neural groove stage is 2.4 mm., and the average diameter of the outer envelope is 4.9 mm. Hatchlings have large, conical oral discs, heavy gills, and a large amount of yolk; their average total length is 6.3 mm.

Tadpoles have been found in pools in clear streams; some tadpoles have been observed to cling by their mouths to rocks in the stream; others were found on the bottom where they seek refuge among pebbles or under rocks and leaves. A complete developmental series of tadpoles is not available. Eleven tadpoles in stage 25 of development have body lengths of 8.3 to 10.2 mm. (9.3 mm.), tail lengths of 17.3 to 21.0 mm. (18.8 mm.), and total lengths of 25.9 to 31.0 mm. (28.1 mm.). One tadpole in stage 41 and one in stage 42 have body lengths of 11.5 and 12.5 mm., tail lengths of 27.2 and 29.5 mm., and total lengths of 38.7 and 42.0 mm., respectively. The snout-vent lengths of two specimens in stage 43 and one in stage 45 are 12.7, 13.0, and 13.6 mm., respectively.

A typical tadpole in stage 25 of development (KU 80620 from Finca La Sumbadora, Panamá) has a body length of 9.5 mm., tail length of 19.0 mm., and a total length of 28.5 mm.; body only slightly wider than deep, nearly flat dorsally; snout broadly rounded in dorsal view, bluntly rounded in lateral view; eyes widely separated, directed dorsolaterally; nostril slightly closer to eye than to tip of snout; mouth ventral; spiracle sinistral, located about two-thirds distance from snout to posterior edge of body; anal tube dextral; caudal musculature moderately heavy, straight; dorsal fin not extending onto body; fins deepest at about two-fifths length of tail, where depth of caudal musculature about equal to depth of dorsal and depth of ventral fin; musculature

extending nearly to tip of tail; body dark grayish brown above and pale grayish tan below with small dark brown spots dorsally and white flecks laterally; caudal musculature pale tan with dark brown flecks over entire surface and dark brown streaks on posterior one-half of ventral fin and on all of dorsal fin (Fig. 14B). Median one-third of upper lip bare; rest of mouth bordered by a single row of conical papillae; lateral fold present; tooth rows ⅔; upper rows cone-shaped, about equal in length, broadly /\-shaped; second upper row narrowly interrupted medially; lower rows complete, about equal in length, but slightly shorter than upper rows; upper beak moderately massive, its inner surface forming a continuous arch with short lateral processes; lower beak broadly \/-shaped; both beaks finely serrate (Fig. 15D).

Tadpoles from El Volcán, Chiriquí (KU 91833), are more heavily pigmented than those from Finca La Sombadora; the spots on the tail are larger. In life these tadpoles had dark brownish black bodies with golden and green lichenous flecks; the tail was tan with dark brown markings, and the iris was a grayish bronze color. In life tadpoles from Finca La Sumbadora were olive-tan above and dark gray with pale bluish gray irridescent spots ventrally. The caudal musculature was creamy tan with brown flecks and streaks, and the iris was pale bronze.

Metamorphosing young have been found on vegetation at the edge of streams and have been raised in the laboratory. Seven recently metamorphosed young have snout-vent lengths of 13.6 to 15.6 mm. (14.6 mm.). A living juvenile (KU 91913) raised in the laboratory from a tadpole obtained at Finca La Sumbadora had a brown dorsum with darker brown markings, a white spot below the eye, and a narrow white labial stripe. The belly was white; the flanks were brown with white spots, and the posterior surfaces of the thighs were yellowish tan. The iris was a golden bronze color with much black reticulation.

Remarks.—This species has been confused with *Smilisca sordida;* most authors have referred both species to *Hyla* (*Smilisca*) *gabbi.* Examination of the types of *Hyla sordida, gabbi, salvini,* and *nigripes* revealed that all of the names were referable to a single species (*S. sordida*), and that the small, blunt-snouted species in Panamá and southern Costa Rica probably was without a name. Possibly *Hyla molitor* Schmidt (1857) is based on the species that we have named *S. sila,* but several discrepancies in his description, plus the unknown provenance of the type, have led us to discount the applicability of that name to the species under consideration.

Distribution.—*Smilisca sila* ranges along the Pacific slopes and lowlands of southern Costa Rica and Panamá at elevations from sea level to about 1300 meters; in northern South America the species occurs in the Carribean lowlands and in the valleys of the northward draining rivers of Colombia (Fig. 3).

Specimens examined, 234, as follows: Costa Rica: **Puntarenas:** 6 km. E Golfito, KU 91717; Quebrada Boruca, 22 km. E Palmar Norte, KU 64265-6; Río Zapote, 7 km. E Palmar Norte, USC 7100 (2). **San José:** San Isidro el General, KU 28200; 14 km. NW San Isidro el General, USC 7098 (2); 15 km. WSW San Isidro el General, USC 7097.

Panama: **Canal Zone:** Barro Colorado Island, AMNH 62320-3, CNHM 13324, 13326-8, 13330, 13338, 13359, 13423-5, KU 80460-6, 80619 (young), 80625 (skeleton), UMMZ 63542-6, USC 7051. **Chiriquí:** Boquete, AMNH 69815, UMMZ 58441-5; El Volcán, KU 77413, 91828-31 (skeletons), 91852-74, 91832 (eggs), 91833 (tadpoles); 6 km. S El Volcán, CNHM 60442; 16 km. NNW El Volcán, KU 91879-90; Finca Palosanto, 6 km. WNW El Volcán,

KU 77406-12, 77692 (skeleton), 91875-7, 92330-1; Río Colorado, 17 km. NNW El Volcán, KU 91878, 92332; Valle Hornito, 19 km. NE Gualaca, KU 92333-45. **Coclé:** El Valle, AMNH 55440-5 (13), 59607-14, CNHM 48140, 60349-2, 60387-92, 60401-4, 60443, 67842-5, KU 91834 (young), 91902-4, TNHC 23751-2, USNM 140653. **Colón:** Río Candelaria, AMNH 53708-15, CNHM 67826-36. **Darién:** Camp Creek, Camp Townsend, AMNH 40756-7, 40936-9, 40992; Río Chico, AMNH 39784, 40986-7; Río Pita, CNHM 67823-5; Tacarcuna, USNM 141796-802; Three Falls Creek, AMNH 41684, 51788. **Los Santos:** Cerro Hoya, USNM 148213-4; Lajamina, Río Puria, KU 67915. **Panamá:** Altos de Pacora, KU 91894; Cerro Jefe, KU 91895-6; Cerro La Campana, CNHM 67846, KU 91897-900, USNM 139689; Finca La Sumbadora, KU 80467-81, 80620 (tadpoles), 91910 (eggs), 91911-2 (tadpoles), 91913 (young), 91908-9 (skeletons); Río Calobra, USNM 53722, Río Pacora, 9 km. NNE Pacora, KU 91901. **Veraguas:** Cerro Carbunco, USNM 129066; Cerro Tute, CNHM 67837-41; Isla Cebaco, Río Platanal, KU 91891-3.

Colombia: **Antioquia:** Urabá, Villa Arteaga, CNHM 63893 (Goin). **Atlantico:** Sabanalarga, Río Causa, AMNH 14506.

Smilisca sordida (Peters), new combination

Hyla sordida Peters, Monatsb. Konigl. Akad. Wissen. Berlin., p. 460, 1863 [Syntypes.—ZMB 3141 (two specimens) from "Veragua," Panamá; J. von Warszewicz collector]. Brocchi, Mission scientifique au Mexique . . ., pt. 3, sec. 2, Études sur les batrachiens, p. 42, 1881. Boulenger, Catalogue Batrachia Salientia in British Museum, p. 393, Feb. 1, 1882. Günther, Biologia Centralia-Americana: Reptilia and Batrachia, p. 273, Sept. 1901. Nieden, Das Tierreich, Amphibia, Anura, I, p. 258, June, 1923.

Hyla gabbi Cope, Jour. Acad. Nat. Sci. Philadelphia, new ser., 8, pt. 2:103, 1876 [Syntypes.—USNM 30658-9 from near Sipurio, Limón, Costa Rica; William M. Gabb collector]. Brocchi, Mission scientifique au Mexique . . ., pt. 3, sec. 2, Études sur les batrachiens, p. 37, 1881. Boulenger, Catalogue Batrachia Salientia in British Museum, p. 372, Feb. 1, 1882. Cope, Bull. U. S. Natl. Mus., 32:32, 1887. Günther, Biologia Centrali-Americana: Reptilia and Batrachia, p. 274, Sept. 1901. Werner, Abhand. Konigl. Akad. Wissen. München., 22:351, 1903. Nieden, Das Tierreich, Amphibia, Anura I, p. 252, June, 1923. Taylor, Univ. Kansas Sci. Bull., 35(1):840, July 1, 1952. Cochran, Bull. U. S. Natl. Mus., 220:54, 1961.

Hyla nigripes Cope, Jour. Acad. Nat. Sci. Philadelphia, new ser., 8, pt. 2:104, 1876 [Syntypes.—USNM 30685-6, from Pico Blanco, Costa Rica; William M. Gabb collector]. Brocchi, Mission scientifique au Mexique . . ., pt. 3, sec. 2, Études sur les Batrachiens, p. 38, 1881. Boulenger, Catalogue Batrachia Salientia in British Museum, p. 394, Feb. 1, 1882. Cope, Bull. U. S. Natl. Mus., 32:32, 1887. Günther, Biologia Centrali-Americana: Reptilia and Batrachia, p. 278, Sept., 1901. Nieden, Das Tierreich, Amphibia, Anura I, p. 253, June, 1923. James, Copeia, 3:147, Sept. 30, 1944. Taylor, Univ. Kansas Sci. Bull., 35(1):853, July 1, 1952. Cochran, Bull. U. S. Natl. Mus., 220:56, 1961.

Hyla salvini Boulenger, Catalogue Batrachia Salientia in British Museum, p. 372, Feb. 1, 1882 [Syntypes.—BMNH 1947.2.24.13-14 from Cartago, Costa Rica; Osbert Salvin collector]. Günther, Biologia Centrali-Americana: Reptilia and Batrachia, pl. 71, Fig. B., Sept., 1901. Werner, Abhand. Zool.-Bot. Gesell. Wien, 46:8, Sept. 30, 1896.

Smilisca gabbi, Starrett, Copeia, 4:303, Dec. 30, 1960.

Diagnosis.—Size moderate (♂ 45 mm., ♀ 64 mm.); skull slightly wider than long, having large and elongate frontoparietal fontanelle; supraorbital flanges absent; squamosal small, not contacting maxillary; bony section of ethmoid terminating just anterior to anterior edge of orbit; tarsal fold weak, full length of tarsus; inner metatarsal tubercle long, low, flat, elliptical; lips thin and flar-

ing; fingers one-half webbed; toes four-fifths webbed; diameter of tympanum about one-half that of eye; no white labial stripe; dorsal dark markings irregular, sometimes forming broad transverse bars; pale flecks on flanks and usually on posterior surfaces of thighs; vocal sacs in breeding males white. (Foregoing combination of characters distinguishing S. *sordida* from any other species in genus.)

Description and variation.—Ten breeding males from 15 to 20 kilometers west-southwest of San Isidro el General, San José, Costa Rica, have snout-vent lengths of 38.1 to 42.6 mm. (40.5 mm.). In these specimens, the tibia/snout-vent length ratio is 0.50 to 0.54 (0.52), and the tympanum/eye ratio is 0.45 to 0.57 (0.49). Specimens from the Pacific slopes of Costa Rica are larger than those from the Meseta Central and the Caribbean lowlands. Ten males from 6 kilometers east of Golfito, Puntarenas, have snout-vent lengths of 38.4 to 44.6 mm. (41.8 mm.), and five males from Rincón, Peninsula de Osa, have snout-vent lengths of 38.8 to 41.6 mm. (40.3 mm.). Snout-vent lengths of ten males from La Fortuna, Alajuela, are 31.9 to 36.0 mm. (34.4 mm.), of ten males from Pandora, Limón, 33.8 to 37.6 mm. (35.9 mm.), and of ten males from Escazú and Río Jorco on the Meseta Central, 34.3 to 37.6 mm. (36.0 mm.). Eight females from the Río Jorco on the Meseta Central have snout-vent lengths of 48.8 to 53.8 mm. (50.4 mm.), and six females from various localities on the Pacific slopes of Costa Rica have snout-vent lengths of 56.5 to 64.0 mm. (59.8 mm.). The only noticeable differences in proportions between males and females is in the tympanum/eye ratio; for example, this ratio is 0.47 to 0.53 (0.49) and 0.54 to 0.68 (0.61) in ten males and eight females, respectively, from the Meseta Central.

The shape of the snout and the associated cranial elements of S. *sordida* vary geographically and ontogenetically. Specimens from the Caribbean lowlands have blunt snouts in lateral view; those from the Pacific lowlands have longer, more slender snouts that are pointed in lateral view, and those from the Meseta Central are intermediate in snout shape between the two lowland populations (Fig. 4). These differences in shape of the snout are dependent on the nature of the underlying cranial bones, principally the maxillaries and nasals. In specimens from the Caribbean lowlands the nasals are long, wide, and narrowly separated from the ethmoid; the anterior edge is just posterior to the nostril. The maxillary flanges are nearly vertical. In specimens from the Pacific lowlands the nasals are relatively shorter, narrower, and rather widely separated from the ethmoid; the anterior edges of the nasals do not extend so far forward as in specimens from the Caribbean lowlands. The maxillary flanges slant medially. In these cranial characters, specimens from the Meseta Central are intermediate between the two lowland populations.

Superimposed on this geographic variation are ontogenetic changes, which are most noticeable in males. In smaller, and presumably younger, specimens the snouts are more pointed than in larger specimens; consequently some small males from the Caribbean lowlands resemble larger males from the Pacific lowlands, since the nasals and maxillaries of the former are not fully ossified. In addition, in small breeding males the ethmoid is only about one-half ossified, a large frontoparietal foramen is present, the anterior arm of the squamosal extends only about one-fourth the distance to the maxillary (two-thirds the distance in larger specimens), and the tegmen tympani are short, as compared with the long, thin elements in larger specimens.

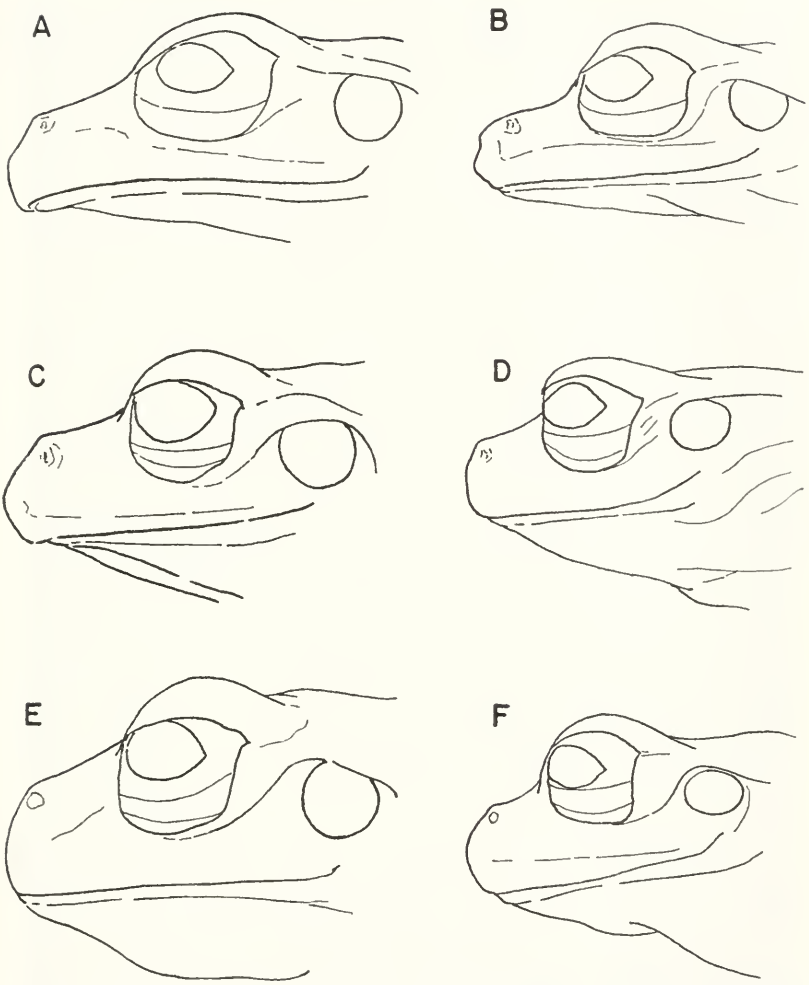


FIG. 4. Variation in the shape of the snout in *Smilisca sordida;* left column females, right column males; all from Costa Rica: (A) Camp Seattle, Rincón de Osa, Puntarenas Prov. (UMMZ 123684); (B) Quebrada Agua Buena, 3 km. SW Rincón de Osa, Puntarenas Prov. (USC 7236); (C) Río Oro, 28.5 km. NW Villa Neily, Puntarenas Prov. (KU 91742); (D) Río Jorco, near Desamparados, San José Prov. (KU 91765); (E-F) Bambú, Limón Prov. (USC 7183). ×3.

The dorsal ground-color of *Smilisca sordida* is gray to pale tan or reddish brown; the venter is white. The dorsum is variously marked with dark gray, dark brown, reddish brown, or olive-green spots or blotches (Pl. 7C). A dark interorbital bar usually is present. The dorsal markings on the body usually consist of a blotch, or two or more spots, on the occiput, in the scapular region, and in the sacral region. In many specimens, especially females, these markings are in the form of broad transverse bars. A female (USC 7164) from

Las Cañas, Guanacaste, Costa Rica, has a tan dorsum with many black flecks and round brown spots bordered by darker brown. One female (KU 91763) from the Río Jorco, San José, Costa Rica, has a unicolor tan dorsum. Some individuals have scattered, small white spots on the dorsum; these are most evident in a male (USC 7153) from La Fortuna, Alajuela. White labial stripes and anal stripes are absent in all specimens.

The limbs are marked by dark brown transverse bars; these are indistinct in some specimens from the Meseta Central and Caribbean lowlands, whereas they are distinct in all specimens from the Pacific lowlands. Specimens from the Caribbean lowlands have two to six bars on each shank, whereas specimens from the Pacific slopes have four to six bars on each shank, and specimens from the Meseta Central have as many as eight bars on each shank. A narrow, sometimes broken white line is present on the ventrolateral edge of the forearm. The webbing on the hand is tan or pale gray, and the ventral surfaces of the tarsi and the webbing on the feet are dark gray or brown. Breeding males have dark brown nuptial excrescences on the prepollex.

The flanks and posterior surfaces of the thighs usually are marked by bluish white and creamy tan flecks, respectively, but vary considerably. In specimens from the Caribbean lowlands a small amount of flecking is present in the inguinal region, and on the posterior surfaces of the thighs flecks are few or absent. In specimens from the Meseta Central, numerous large flecks or small, round spots (pale bluish white in life) are on the posterior half of the flanks; small flecks are on the posterior surfaces of the thighs. Specimens from the Pacific slopes and lowlands of southern Costa Rica (Puntarenas and San José Provinces) have bold mottling of black and bluish white on the flanks and many bluish white flecks on the posterior surfaces of the thighs. The flanks are reticulated from the axilla to the groin in two females (UMMZ 123684 and USC 7236) from Rincón, Peninsula de Osa. In specimens from the Pacific slopes of Guanacaste in northwestern Costa Rica, flecks are present in the inguinal region; indistinct flecks are on the posterior surfaces of the thighs.

The throat is immaculate in specimens from the Caribbean lowlands in Limón Province; the throats are dusky laterally in most other specimens except some from the Meseta Central, in which the throats are heavily flecked with black. This variation occurs in males and females.

The color and pattern in life are highly variable. A composite description of living individuals (now KU 91718-41) from 6 kilometers east of Golfito, Puntarenas, Costa Rica, illustrates the variability: "Dorsum pale olive-green, fading to tan posteriorly, or tan all over with dark olive-green or dark brown spots on back and bars on limbs. Flanks dark brown with cream, greenish gray, or bluish gray mottling. Posterior surfaces of thighs dark brown with pale blue, pale green, or tan flecks. Iris creamy silver. Throats white with some brown flecks peripherally." (Duellman, Field notes, February 15, 1965.) A male from the Río Jorco, San José, Costa Rica, was dull olive-tan above with olive-green marks; the flanks were brown with pale tan flecks, and the posterior surfaces of the thighs were pale brown with cream-colored flecks. Six females from the same locality were reddish brown above with olive-brown or dark brown markings; one was uniform orange-tan, and another was dull olive-green with darker markings.

The color of the iris in living frogs varies from creamy silver to grayish yellow or bronze with a variable amount of black reticulation.

Natural History.—Smilisca sordida is not associated with any one type of vegetation; instead it lives in the vicinity of rocky streams having low gradients. Breeding takes place primarily in the dry season, when the water in the streams is clear and at a low level. Through most of the range of *S. sordida* showers, or even short heavy rains, occur in the dry season. After such rains the breeding activity is maximal. Breeding congregations have been found from December through April, but a few calling males and gravid females have been taken in June, July, and August. In the rainy season non-breeding individuals are found sitting on bushes near streams at night. Taylor (1952: 843) found specimens in bromeliads by day.

Males usually call from rocks or gravel bars in, or at the edge of, streams. Some individuals perch in low bushes overhanging the streams, and some sit in shallows in the streams. Clasping pairs have been found on the banks of streams and in shallow water in streams.

The breeding call consists of one to six moderately short, rather high-pitched notes (duration 0.18 to 0.45 seconds) repeated at intervals of 12 seconds to several minutes. Each note is a vibrant rattle having 78 to 135 pulses per second and major frequences of about 1200 to 2600 cycles per second (Pl. 11C).

The tadpoles live in shallow parts of the streams, where they cling to the surfaces of small rocks and hide beneath leaves and rocks. A complete developmental series of tadpoles is not available; measurements of those stages examined are summarized in Table 12.

A typical tadpole in stage 36 of development (KU 68475 from 15 km. WSW of San Isidro el General, Costa Rica) has a body length of 11.7 mm., tail length of 22.8 mm., and a total length of 34.5 mm.; body about three-fourths as deep as wide; snout broadly rounded in dorsal view, sloping and rounded in lateral view; eyes widely separated, directed dorsolaterally; nostril slightly closer to eye than to tip of snout; mouth ventral; spiracle sinistral, about two-thirds distance from snout to posterior end of body and slightly below mid-line; anal tube dextral; caudal musculature heavy, straight; dorsal fin not extending onto body; fins deepest at about mid-length of tail; there depth of caudal musculature equal to depth of dorsal fin and half again as deep as ventral fin; musculature extending nearly to tip of tail; body reddish brown above and pale grayish brown with white flecks below; caudal musculature pale tan with brown flecks; a series of reddish brown dashes at base of caudal fin separated from others in series and from dashes on other side by creamy white; fins transparent with reddish brown flecks on posterior one-half of ventral fin and on all of dorsal fin (Fig. 14C). Mouth bordered by two rows of short, pointed papillae; lateral fold present; tooth-rows 2/3; upper rows equal in length; second upper row narrowly interrupted medially; three lower rows complete, nearly as long as upper rows, deeply indented medially; upper beak robust, inner surface not forming continuous arch with short lateral processes; lower beak deep, V-shaped; both beaks bearing short serrations (Fig. 15F).

Little variation occurs in structure. In some specimens the second upper tooth-row is complete; no individuals were found to have the row broadly interrupted medially.

The series of dark dashes on the dorsal edge of the caudal musculature is diagnostic of all stages studied. In life, tadpoles from 15 and 20 kilometers west-southwest of San Isidro el General, Costa Rica, had a tan body, often

with an olive-tan tinge; the caudal musculature was tan; the flecks and dashes were dull red or reddish brown. Tadpoles from 6 kilometers east of Golfito, Costa Rica, had bodies with olive-green flecks. The caudal musculature was brown with bluish green flecks; the fins were transparent with reddish brown flecks. The belly was a silvery golden color. Tadpoles from Bajos de Jorco, Costa Rica, had brown bodies with bluish green flecks; the tail and fins had reddish brown flecks and dashes. The iris was a bronze color in specimens from all three localities, as well as in the young mentioned in the following paragraph.

Nine recently metamorphosed young were found on vegetation at the edges of streams in April. These specimens have snout-vent lengths of 13.1 to 15.7 mm. (14.9 mm.) and in life were pale greenish tan or olive-tan above and white below. The hands, feet, and thighs were pale yellowish tan.

Remarks.—The foregoing synonymies indicate that confusion has existed in the application of various names to this species, as well as in use of the names *sordida* and *gabbi* to include the species that we describe and name *Smilisca sila*. Correct allocation of the names involved was possible only after studying and comparing the type specimens, for the descriptions given by the various authors are not sufficiently explicit to determine the nature of many essential features.

The presence of a rounded snout and a long white throat in males distinguishes *S. sordida* from *S. sila*, which has a high truncate snout and short dark throat in males. The two syntypes of *Hyla sordida* Peters, 1863, (ZMB 3141) are males having snout-vent lengths of 36.9 and 37.0 mm. The two syntypes of *Hyla gabbi* Cope, 1876 (USNM 30658-9), are females having snout-vent lengths of 52.8 and 53.7 mm., respectively. Also included in the collections made by Gabb is eastern Costa Rica are two males (USNM 30685-6), which Cope (1876) named and described as *Hyla nigripes*. These specimens are soft and faded, but are recognizable as the same as *Hyla sordida* Peters; the syntypes of *Hyla nigripes* have snout-vent lengths of 37.6 and 37.7 mm. We have examined one of the syntypes of *Hyla salvini* Boulenger, 1882 (BMNH 1947.2.24.13), a female having a snout-vent length of 54.6 mm. We are convinced that all of these type specimens are representatives of one species, the earliest name for which is *Hyla sordida* Peters, 1863. The type localities for three of the named species are in Costa Rica—*H. gabbi* from Sipurio on the Caribbean lowlands, *H. nigripes* from the Caribbean slopes of Pico Blanco, and *H. salvini* from Cartago on the Meseta Central. The type locality of *H. sordida* was given as "Veraguas" by Peters (1863). At that time Veraguas was often considered to be most of western Panamá. Though we have not seen Panamanian specimens other than the types of *S. sordida* and one specimen from the Pacific lowlands of western Panamá, the species probably occurs on the Caribbean slopes of western Panamá. The species has been taken on the Caribbean lowlands of Costa Rica within a few kilometers of Panamá; collecting on the Caribbean slopes in the provinces of Bocas del Toro and Veraguas should reveal the presence of *Smilisca sordida* there.

Distribution.—*Smilisca sordida* is found along the Pacific slopes and lowlands from Guanacaste, Costa Rica, southeastward to extreme western Panamá, to elevations of about 1200 meters on the Meseta Central in Costa Rica, and on the Caribbean slopes and lowlands of Costa Rica and probably adjacent Panamá (Fig. 5). One specimen purportedly comes from "Río Grande, Nicaragua."

FIG. 5. Map showing locality records for *Smilisca sordida*.

Specimens examined.—412, as follows: NICARAGUA: "Río Grande" (? Depto. Zelaya), MCZ 2634.

COSTA RICA: **Alajuela:** Between Atena and Salto de San Mateo, USC 6185; 8 km. N Ciudad Quesada, USC 7155 (4); La Fortuna, USC 7153 (20); 3 km. E La Fortuna, USC 7150; San Carlos, USNM 29969; Sarchi, KU 32990-9, 36792-3.

Cartago: Cartago, BMNH 1947.2.24.13; headwaters of Río Pacuare, USC 119; Instituto Interamericano de Ciéncias Agricolas, Turrialba, KU 37012, USC 420, 437; Río Reventazón, Turrialba, MCZ 29268; 10 km. N Río Reventazón bridge, USC 7073; 5 km. SW Río Reventazón bridge on Paraiso-Orosi road, USC 669; Turrialba, UMMZ 118405, USC 455, USNM 29936-9.

Heredia: Puerto Viejo, KU 36791.

Guanacaste: Las Cañas, USC 7164; Santa Cecilia, MCZ 7924-5; Tilarán, USC 7161 (5).

Limón: Bambú, USC 7171 (2), 7183 (13); La Lola, USC 820 (6), 6083-94, 8064, 8071; Pandora, USC 7188 (7), 7189, 7190 (3), 7191 (5); Pico Blanco, USNM 30685-6; Río Larí, 14-16 km. SW Amubre, USC 7179, 7180 (10); Sipurio, USNM 30658-9; Suretka, KU 36764, 36765 (skeleton), 36766-78.

Puntarenas: 6 km. N Dominical, KU 91749-50, 91811 (young), 91812 (tadpoles); Esparta, MCZ 8028; 6 km. E Golfito, KU 91718-41, 91809 (young), 91810 (tadpoles), 91816-9 (skeletons), USC 7103 (23); Quebrada Agua Buena, 3 km. SW Rincón de Osa, USC 7236 (6); Quebrada Boruca, 22 km. E Palmar Norte, KU 64264; Rincón de Osa, Camp Seattle, UMMZ 123680-5, S-2792

(skeleton), USC 705 (5), 6023, 7254; Río Barranca, USC 7119 (2); Río Ceiba, 6 km. NW Buenos Aires, KU 91747-8, USC 7112 (7); Río Ciruelitas, 16 km. NW Esparta, USC 7121 (3); Río Claro, 14.2 km. NW Villa Neily, USC 7110 (4); Río Ferruviosa, 7 km. S Rincón de Osa, USC 7235 (4); Río Lagarto at Pan-American Hwy. (Guanacaste Border), USC 7122 (4); Río La Vieja, 30 km. E Palmar Norte, KU 87684 (tadpoles), 91743-6, USC 7083 (2); Río Oro, 28.5 km. NW Villa Neily, KU 91742; Río Volcán, 10 km. W Buenos Aires, USC 7113; Río Zapote, 7 km. E Palmar, USC 7100 (4); 3-5 km. W Palmar, USC 7101 (18); 7 km. SE Palmar, KU 64261-3; 1.2 km. NW Villa Neily, USC 8032; 3 km. NW Villa Neily, USC 7109 (20); 5 km. NW Villa Neily, USC 6176, 8035.

San José: Bajos de Jorco, KU 91813 (tadpoles); Escazú, KU 34863, 34869-75, USC 813; between Monrovia and La Hondura, ± 0.5 km. N Santa Rosa, USC 302 (2); Paso Ancho, Río Jorco, UMMZ 122649 (6), USC 530 (3); Río Jorco, near Desamparados, KU 91757-65, 91796-7, 91820-3 (skeletons), USC 228, 513, 7117 (7); Río Peje, 10 km. SSE San Isidro el General, USC 7115 (3); Río Tiriví, MCZ 7972; San Isidro el General, CNHM 101096, KU 28201, 32989, UMMZ 72024; 15 km. WSW San Isidro el General, KU 64245-56, 68473 (tadpoles), 68474 (young), 68475 (tadpoles), 86516, 91754-6, 91793-5, USC 7097 (6); 17.1 km. WSW San Isidro el General, USC 6047; 18 km. WSW San Isidro el General, USC 689; 20 km. WSW San Isidro el General, KU 64257-9, 64260 (skeleton), 68468 (young), 68469 (tadpoles), 68470 (young), 68471-2 (tadpoles), 68476 (young), 68633-4 (skeletons), 91751-3; San José, AMNH 7501-4, USC 298; Santa Rosa, Río Virilla, USC 7145.

Panama: Chiriquí: Río Jacu, 5.8 km. ESE Paso Canoas, KU 91905. "Veraguas," ZMB 3141 (2).

ANALYSIS OF MORPHOLOGICAL CHARACTERS

Osteology

In attempting to assay the taxonomic significance of skeletal differences we are faced with a dearth of data on the skeletons of frogs in general and hylids in particular. Recent reviews by Brattstrom (1957) and Hecht (1962, 1963) have been concerned with general salientian classification and phylogeny, principally at the family level. Savage and Carvalho (1953), Griffiths (1959), and Baldauf (1959) used osteological characters in determining the taxonomic status of the families Pseudidae, Brachycephalidae, and Bufonidae, respectively. Carvalho (1954) presented osteological evidence for the generic separation of New World microhylids. Zweifel (1956) and Tihen (1962) used osteological characters at the levels of the species-group and species in their respective studies on *Scaphiopus* and *Bufo*. Little has been recorded about the skeletons of the hylids. Goin (1961) mentioned dentigerous elements and cranial co-ossification in his synopsis of the genera of hylids. Copland (1957) in his review of the *Hyla* of Australia, Funkhouser (1957) in her revision of *Phyllomedusa*, and Zweifel (1958) in his review of *Nyctimystes* did not consider skeletal characters.

Some osteological studies on hylids have yielded worthwhile information. Mittleman and List (1953) used osteological characters in defining the genus *Limnaoedus:* Starrett (1960) used cranial characters in combination with jaw musculature in defining the genus *Smilisca,* and Duellman (1964) used cranial characters in delimiting the *Hyla bistincta* group. Brief descriptions of cranial structure were given for *Phrynohyas* (Duellman, 1956) and *Ptychohyla* (Duellman, 1963a); specific and sexual differences in the skulls of *Hyla chaneque* and *Hyla taeniopus* were pointed out by Duellman (1965). Stokely

and List (1954) described early cranial development in the hylid *Pseudacris triseriata triseriata*.

Because our knowledge of the skeleton in hylids is so incomplete, we are not attempting to place *Smilisca* in the general scheme of hylid phylogeny on the basis of skeletal characters. Instead, our purposes are to describe the skeleton and its ontogenetic development in one member of the genus (*S. baudini*), and to make comparisons that show taxonomic differences in osteological characters among species of *Smilisca*.

The study of 68 dried skeletons and 25 cleared and stained preparations, including an ontogenetic series of *S. baudini*, has resulted in an understanding of the progressive development of skeletal elements and a knowledge of interspecific and intraspecific variation in these elements. Furthermore, investigations of the osteology have provided correlations between some cranial characters and certain aspects of external morphology.

Descriptive Osteology of Smilisca baudini

The following description is based primarily on an adult female (KU 68184):

Skull.—The skull is large, solid, and broader than long; the greatest width is between the sutures of quadratojugal and maxillary on either side of the skull (Pls. 2-3). The maxillaries bear well-developed dorsal flanges, curve gently, join the moderately convex premaxillaries anteriorly and form a slightly truncate snout. The combined premaxillary width is about one-fourth the width of the skull. The premaxillaries are separated medially, and laterally from the maxillaries by sutures. Each premaxillary bears a dorsomedial alary process, which is anteriorly convex and four times as high as the depth of the lateral wing of premaxillary; each premaxillary also has a ventromedial palatine process that projects dorsally from the lingual edge of the premaxillary. The septomaxillaries are closely associated dorsally with the premaxillaries immediately lateral to the prenasal processes.

The nasals are large, widest anteriorly and narrowing posteriorly, parallel to maxillaries, and not separated from the ethmoid by cartilage. The nasals bear long, delicate maxillary processes extending nearly to the maxillaries. Anteriorly, the nasals are widely separated by the partially ossified internasal septum, which is in contact with the premaxillaries between the prenasal processes; the anterior points of the nasals lie approximately one-half the distance between the anterior ends of the ethmoid and the premaxillaries. The ethmoid is large and completely ossified; the margins are smooth. The trunate anterior edge lies between the nasals and is in contact with the internasal septum. The frontoparietals are large, smooth-margined, and bear large supraorbital flanges curving posterolaterally at the rear of the orbit. A small, oval foramen involves the posterior part of the ethmoid and anterior portion of frontoparietals; continued ossification in older specimens fills in the foramen, thereby resulting in a solidly roofed cranium. The auditory regions are relatively massive and bear narrow tegmen tympani; the distal ends of the tegmen tympani are medial to the lateral edge of the pterygoids in dorsal view. The squamosals are large; the long anterior arm is separated from the maxillary by a suture. The delicate, spindle-shaped columellae lie ventral to the tegmen tympani and squamosals, are spatulate distally, and have a broad basal attachment to the auditory region.

The vomers are moderately large and are in contact anteriorly with the premaxillaries and posteriorly with the ethmoid. Each vomer has two wide serrated flanges laterally. The tooth-bearing parts of the vomers are widely separated and at a slight angle to one another; the vomers terminate medially in two pointed processes on the ethmoid. The palatines are edentate, but bear strong ridges throughout their lengths. They are broadly in contact with the maxillary, are narrow medially, and are attached by pointed processes to

the medial part of the ethmoid. The pterygoids are large, attached to the maxillaries immediately anterior and medial to the squamosal-maxillary connection, bear well-developed pedicles, which are broadly attached to the proötic, and a wide wing is in contact posteriorly with the distal two-thirds of the quadrate.

The angular makes up most of the lower jaw, bears a broad articular surface posteriorly, and has a small coronoid process on the lingual edge; anteriorly the angular is separated from the dentary and mentomecklian by Meckel's cartilage. The dentary lies external to the angular and extends from the mentomecklian to approximately the mid-length of the angular. The mentomecklians are ossified, but separated by cartilage medially.

Hyoid.—The hyoid plate is curved, thin, and mostly cartilaginous, but calcified posteriorly (Fig. 6). The anterior cornua are slender, cartilaginous, and curve anteromedially from the hyoid plate and thence laterally and posteriorly, to attach to the posterior surface of the proötics. The lateral cornua are broad, flat, cartilaginous lateral extensions from the bases of the anterior cornua. The posterior cornua are bony, except distally.

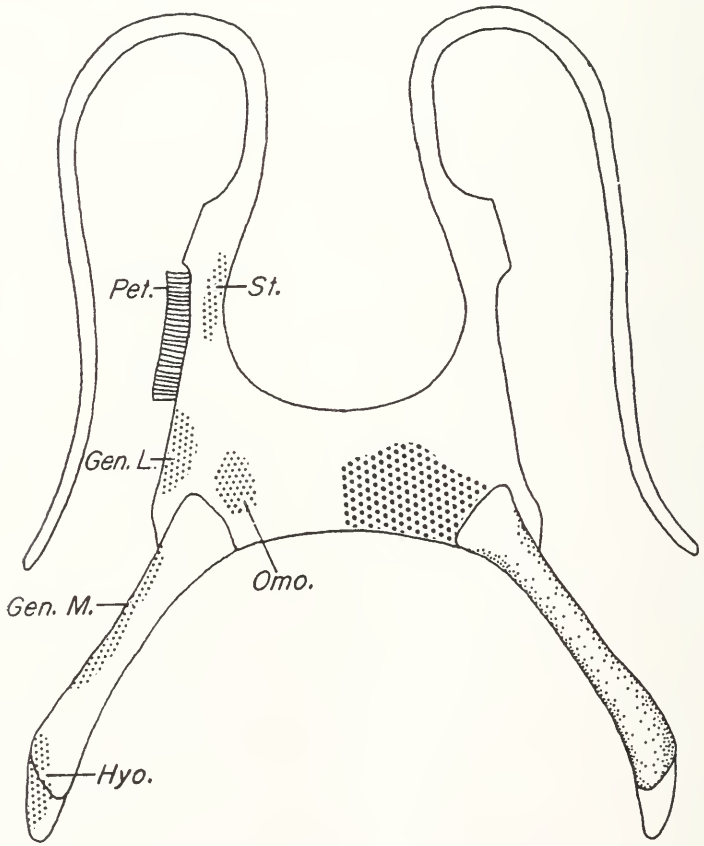


FIG. 6. Ventral view of hyoid apparatus of an adult male *Smilisca baudini* showing areas of muscle attachment: *Gen. L.*, attachment of geniohyoideus lateralis; *Gen. M.*, attachment of geniohyoideus medialis; *Hyo.*, attachment of hyoglossus; *Omo.*, attachment of omohyoideus; *Pet.*, petrohyoideus; *St.*, attachment of sternohyoideus. KU 64220, ×5.

Vertebral Column.—The atlas lacks transverse processes and a neural crest, whereas transverse processes are present on the other seven presacral vertebrae, and knoblike neural crests are present on the second, third, and fourth vertebrae; a faint neural ridge is visible on the fifth vertebra. The transverse processes are directed laterally on the second and sixth vertebrae, ventrolaterally on the third, posterolaterally on the fourth and fifth, and anterolaterally on the seventh and eighth. The processes are slightly expanded on the fourth, and more so on the fifth, vertebra. The sacral diapophyses are expanded and have a border of calcified cartilage laterally. There are two sacral condyles. The slender coccyx has a thin dorsal ridge on the anterior three-fourths of its length.

Pectoral Girdle.—The omosternum is large, ovoid, and cartilaginous; the sternum is a thin cartilaginous sheet deeply notched posteriorly and is not differentiated into episternal and xiphisternal elements. The coracoids are robust, twice as stout as the clavicles. The epicoracoidal cartilages overlap in the usual arciferal manner, except that they are fused anteriorly between the slender clavicles. The clavicles are strongly arched. The clavicle, coracoid, and scapula on each side form a bony articulation at the glenoid fossa. A bifurcation of the ventral end of the scapula results in a large glenoid foramen. The scapula is flat and expanded dorsally; the suprascapula is broad, flat, and calcified in large adults. In young specimens no distinct ossification of the cleithrum or ossification of endochondral centers are evident.

Arm and Hand.—The humerus is equally well-developed in both sexes and has a prominent lateral crest. The radius and ulna are completely fused. A bony prepollex is present in both sexes. The metacarpals are about equal in length. The phalangeal formula is 2-2-3-3; the terminal phalanges are claw-shaped.

Pelvic Girdle.—The ilia are long, slender, and slightly curved. A thin ridge projects laterally from the dorsal edge of the posterior one-half of each ilium. The ilial prominence is large and knoblike when viewed from above. The anterior edge of the ilial prominence is at the level of the anterior edge of the acetabular border. The dorsal acetabular expansion is small. The pubis is slender, and the ischium is elevated and robust.

Leg and Foot.—The slightly curved femur has a distinct crest proximally on the posterior surface. The nearly straight tibio-fibula is slightly longer than the femur. The tibial and fibial elements are completely fused but have a distinct cleft between them. A small foramen exists at the mid-length of the tibio-fibula. The fibulare (calcaneum) is much more robust than the tibiale (astragalus). The prehallux is large and flat. The metatarsals of the third, fourth, and fifth digits are equal in length; the metatarsal of the second is somewhat shorter, and that of the first is much shorter. The phalangeal formula is 2-2-3-4-3; the terminal phalanges are claw-shaped.

Developmental Cranial Morphology of Smilisca baudini

The following description of development of the skull of *Smilisca baudini* is based on the examination of 12 cleared and stained specimens. In table 3 the cranial bones are listed in the left hand column in the approximate order of their appearance in the young frogs. Across the top of the table selected specimens designated by developmental stage or snout-vent length are listed. It should be noted that although each individual, from left to right, has an increasing number of ossified bones, the correlation with increasing size is imperfect; the precise ages of the individuals are unknown.

The first bones to appear are the septomaxillaries, frontoparietals, part of the exoccipital, and the parasphenoid in developmental stage 40. The frontoparietals are represented by two slender ossifications dorsomedial to the orbits; the septomaxillaries are present as small ossifications anterior to the nasal capsules (Pl. 1A). The parasphenoid is present as a faint median ossification, and the exoccipital shows some ossification.

TABLE 3.—THE ORDER OF OCCURRENCE OF CRANIAL OSSIFICATIONS IN THE SKULL OF SMILISCA BAUDINI. WHERE NUMBERS ARE DIVIDED BY A SLASH MARK, THE LEFT AND RIGHT SYMBOLS CORRESPOND TO THE LEFT AND RIGHT SIDES OF THE SKULL, RESPECTIVELY.

BONE	Stage 40	Stage 44	12.6 mm.	13.9 mm.	32.0 mm.	27.0 mm.	20.1 mm.
Frontoparietal	X	X	X	X	X	X	X
Parasphenoid	X	X	X	X	X	X	X
Septomaxillaries	X	X	X	X	X	X	X
Exoccipitals	X	X	X	X	X	X	X
Squamosals	—	X	X	X	X	X	X
Premaxillaries	—	X	X	X	X	X	X
Maxillaries	—	X	X	X	X	X	X
Nasals	—	—	X	X	X	X	X
Pterygoids	—	—	X	X	X	X	X
Vomers	—	—	—	X	X	X	X
Palatines	—	—	—	X	X	X	X
Quadratojugals	—	—	—	X	X	X	X
Ethmoid	—	—	—	—	X	X	X
Columellas	—	—	—	—	X	X	X
Supraorbital Flanges	—	—	—	—	—	X	X
Proötics	—	—	—	—	—	—	X
Vomerine Teeth	—	—	1/1	4/3	5/5	3/3	5/4
Maxillary Teeth	—	0/7	3/5	6/5	30/31	30/26	37/36
Premaxillary Teeth	—	2/4	3/3	5/5	7/6	8/6	8/7

The dentigerous bones are among the most rapidly developed, although not the first to appear. They are present in developmental stage 44 before metamorphosis is completed. The maxillaries bear a few teeth anteriorly and are ossified posteriorly to a point one-third of the distance from the anterior to the posterior edge of the orbit. Ossification lengthens the posterior termini of the maxillaries to the posterior edge of the orbit. In front of the anterior margin of the orbit, bone is proliferated dorsal to the main axes of the maxillaries and forms moderate dorsal maxillary flanges. The premaxillaries appear simultaneously with the maxillaries. Initially they are widely separated medially from each other, and laterally from the developing maxillaries; each bears two or three teeth, large dorsally blunt alary processes, and small

palatine processes. The median and lateral edges of the prenasal processes lengthen heterochronously, causing the median edges to be longest and to lie slightly dorsal to the level of the septomaxillaries. After the maxillaries and premaxillaries develop, the vomers appear as small horizontal ossifications anterior to the parasphenoid. Ossification begins in the lateral flanges, then in the prevomerine processes, and lastly in the posterior dentigerous parts of the bones; the prevomerine processes are the last parts of the vomers to ossify completely.

Initially the frontoparietals are present as thin rods of ossification dorsomedial to the orbits; the frontoparietals extend from the anterior to the posterior end of the orbit by developmental stage 44. The anterior ends of the bones remain thin and pointed; ossification progresses medially from the midpoint of the length of the orbit and posteriorly to the level of the exoccipital; a median center of ossification joins the frontoparietals posteriorly, thereby forming the posterior border of the frontoparietal fontanelle. The supraorbital flanges of the frontoparietals do not appear until all other cranial bones are ossified, or nearly so. The most rapid ossification begins laterally at the posterior edge of the orbit and decreases anteriorly over the posterior half of the orbit. This differential rate of proliferation of bone results in the pattern of development of the supraorbital flanges shown in figure 7. The nasals appear as thin slivers of bone half way between the anterior ends of the frontoparietals and the end of the snout. As ossification proceeds the nasals assume a triangular shape in dorsal view. The anterior ends are pointed; the lateral margins are parallel to the maxillaries. The posteromedial points do not reach the lateral margins of the ethmoid, and the maxillary processes extend about three-fourths the distance from the bodies of the nasals to the maxillaries. Following the union of the frontoparietals posteriorly, the nasals widen anteriorly and are narrower at the midpoints of their long axes than anteriorly or posteriorly. With further ossification the maxillary processes extend to the maxillaries and form complete bony anterior margins to the orbits; the mid-parts of the nasals widen (Pl. 1B).

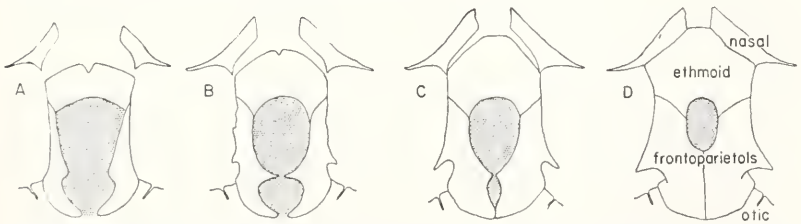


FIG. 7. Developmental sequence of the frontoparietal fontanelle and associated bony elements in *Smilisca baudini:* (A) KU 60026, ×5; (B) KU 85438, ×4; (C) KU 26328, ×3; (D) KU 68184, ×2.3.

The parasphenoid is the first of the palatal bones to appear. At metamorphosis the bone is well developed; the anterior tip is situated just in front of the anterior edge of the orbit, and posteriorly the lateral processes extend laterally beyond the ossified parts of the auditory region. The pterygoids do not appear until metamorphosis, when ossification is evident in only the mid-parts of the posterolateral arms. Ossification follows in the mid-parts of the

anterolateral arms and occurs last in the pterygoid pedicles. The palatines do not appear until all three arms of the pterygoids are at least partly ossified. Ossification proceeds rapidly from the maxillaries medially to the unossified ethmoid, which is the last of the cranial bones to appear. Initially it is extremely shallow; dorsally it is widely separated from the nasals, and ventrally the posterior margin meets the anterior point of the parasphenoid. In dorsal view, ossification proceeds anteriorly between the nasals and posteriorly, ventral to the frontoparietals; ventrally, ossification proceeds posteriorly dorsal to the parasphenoid.

The ventral arms of the squamosal and the supraoccipital region of the exoccipital are the first occipital bones to appear. Ossification follows in the regions of the semicircular canals and occipital condyles. The dorsal end of the ventral arm of the squamosal and the posterior arm of the squamosal ossify as a unit at the same time the quadratojugal appears. Shortly thereafter the anterior arm of the squamosal ossifies, the distal part of the columella appears, and the anterior and lateral parts of the auditory region ossify.

The angular and dentary of the lower jaw appear concurrently with the dentigerous bones. Initially, the angular is short and broad; the articular surface is absent, and the anterior end is slightly overlapped by the dentary. The mentomeckelians do not ossify until approximately the same time that the quadratojugal appears in the upper jaw.

Comparative Osteology

The genus *Smilisca* is characterized by the following combination of cranial osteological characters: (1) A large amount of bone is involved in the skull and a minimal amount of cartilage and/or secondarily ossified cartilage; coossification is absent. (2) The skulls are uniformly broad with angular lateral margins, and truncate anteriorly. (3) An internasal septum and quadratojugals are present. (4) A well-developed squamosal minimally extends one-fourth the distance from the dorsal end of the quadrate to the maxillary, and maximally is separated from the maxillary by a suture. (5) The ethmoid is large; the distance between the anterior end of the ethmoid and the anterior edge of the premaxillary varies between 15 and 20 per cent of the total length of the skull.

On the basis of cranial osteology two species-groups can be recognized within the genus *Smilisca*. The *sordida* group, comprising *S. sordida* and *puma*, is characterized by a broad skull in which the lateral margins of the maxillaries are relatively straight anterior to the orbit. The moderate-sized nasals are rounded anteriorly, and bear relatively short, sometimes blunt, maxillary processes. The long axes of the nasals are not parallel to the maxillaries. The ethmoid is proportionaely small in the *sordida* group. The bony part of the ethmoid terminates near the anterior edge of the orbits and does not extend anteriorly between the nasals; the entire anterior margin of the ethmoid is separated from the nasals by cartilage. The squamosals are generally small. They are narrow in dorsal view, and minimally extend one-fourth the distance from the dorsal end of the quadrate to the maxillary, and maximally, two-thirds the distance. The tegmen tympani are relatively small (Fig. 8).

In contrast to the tendency for reduction of cranial parts in the *sordida* group, the *baudini* group, constituted by *S. cyanosticta, phaeota,* and *baudini,*

is characterized by more ossification of the cranial elements. The skull is broad; the lateral margins are less angular and are gently curved, rather than straight as in the *sordida* group. The nasals tend to be larger with the long axes parallel to the maxillary. Anteriorly the nasals are pointed, and posteriorly

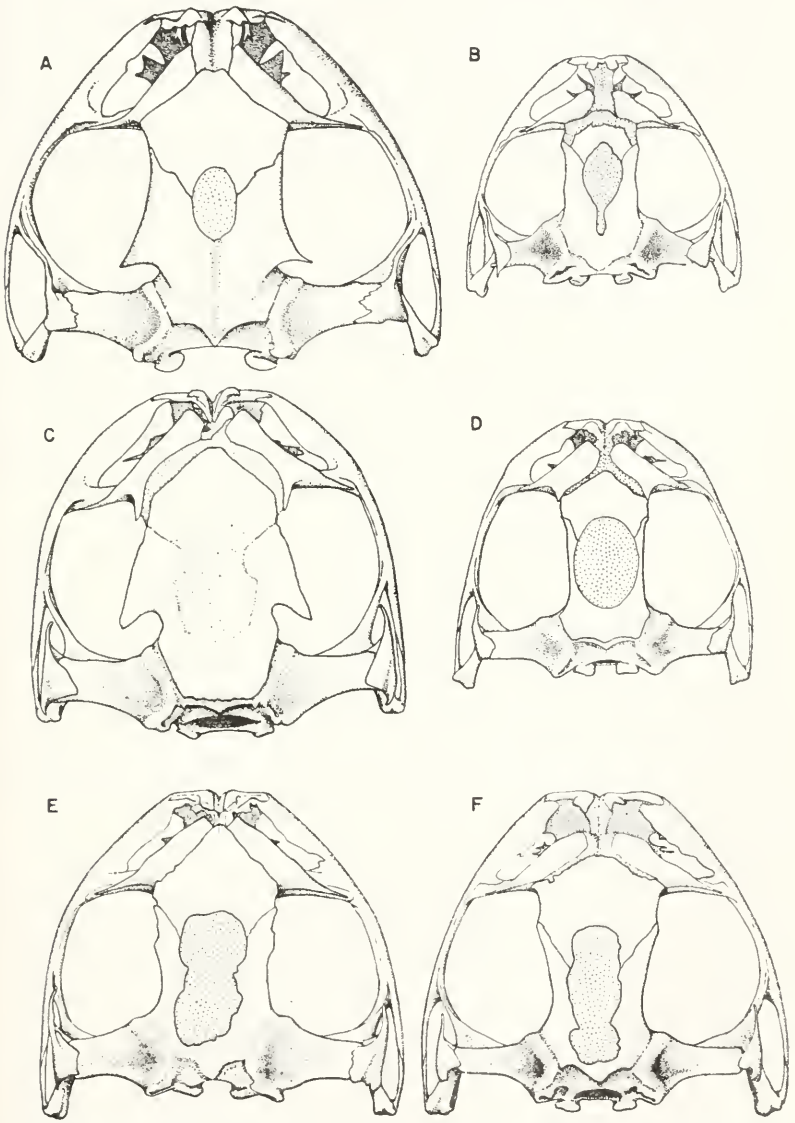


FIG. 8. Dorsal views of the skulls of the species of *Smilisca:* (A) *S. baudini* (KU 68184); (B) *S. puma* (KU 68636); (C) *S. phaeota* (KU 41090); (D) *S. sila* (KU 80625); (E) *S. cyanosticta* (KU 55938), and (F) *S. sordida* (KU 36765). ×1.5.

they bear long, delicate palatine processes extending to the maxillary. The ethmoid is fully ossified, extends anteriorly between the nasals, and laterally is separated by a suture from the nasals if the latter are fully ossified. The squamosals are large, and wide in dorsal view. They minimally extend one-fourth the distance from the dorsal end of the quadrate to the maxillary, and maximally are sutured to the maxillary. The tegmen tympani are massive.

Smilisca sila is intermediate between the two species-groups described. The skull is broad; the lateral margins are gently curved, and have a pronounced angularity just anterior to the palatines which results in a broad, truncate snout. The nasals are moderate in size; because of the anterior angularity of the lateral margins, the long axes of the nasals lie parallel to the maxillary. The nasals are only slightly pointed anteriorly, and posteriorly they bear short, blunt palatine processes and medial processes in contact with the lateral corners of the ethmoid. The ethmoid is fully ossified, but does not extend anteriorly between the nasals. The squamosals are moderate in size and extend one-fourth the distance from the dorsal end of the quadrate to the maxillary. The tegmen tympani are relatively large, but proportionately short.

The cranial characters utilized in the analysis of species groups (general shape, nature of the nasals, ethmoid, squamosals, and tegmen tympani), together with other characters, such as the relative height and shape of the prenasal processes, the extent of the internasal septum, and the nature of the vomers, frontoparietals, maxillaries and pterygoids are useful in distinguishing the various species (Table 4, Fig. 8), as well as in establishing relationships within the species-groups.

Within the *sordida* group, S. *sordida* and S. *puma* can be distinguished by the following characters: The bony part of the ethmoid terminates posterior to the anterior edge of the orbit and is thus widely separated from the nasals by cartilage in S. *puma*. In S. *sordida* the bony part of the ethmoid always terminates at a level equal to, or slightly in front of the anterior edge of the orbit; therefore, less cartilage exists between the ethmoid and nasals in S. *sordida* than in S. *puma*. The width of the premaxillary comprises about 30 per cent of the width of the skull in S. *sordida* and 20 per cent in S. *puma*. The proportion of the length of the skull anterior to the bony part of the ethmoid in S. *sordida* is approximately 21 per cent, as compared with about 29 per cent in S. *puma*. The prenasal processes are convex in S. *sordida* and straight in S. *puma*.

The marked ontogenetic variation in S. *sordida* is considered in more detail in the account of that species, but it is pertinent to the present discussion to note that with respect to some features of the skull some young breeding specimens of S. *sordida* are intermediate in appearance between large females of S. *sordida* and adults of S. *puma*. In some breeding males (usually the smaller individuals) of S. *sordida* the bony part of the ethmoid terminates at the anterior edge of the orbit and is widely separated from the nasals by cartilage. In small individuals S. *sordida*, especially in males, and in adults of S. *puma* the tegmen tympani are relatively short, whereas in adult females of S. *sordida* these elements are long and slender. In the smaller specimens of S. *sordida* and in S. *puma* the squamosal is small; it extends only about one-fourth of the distance to the maxillary in the smaller S. *sordida* and about one-half the distance in S. *puma*. The more massive squamosal in large adult females of S. *sordida* extends at least two-thirds of the distance to the maxillary.

TABLE 4.—COMPARATIVE CRANIAL OSTEOLOGY OF SMILISCA.

CHARACTER	*S. baudini*	*S. cyanosticta*	*S. phaeota*	*S. puma*	*S. sila*	*S. sordida*
Alary Processes	Four times as high as lateral wing of premaxillary; anteriorly convex.	Three times as high as lateral wing of premaxillary; anteriorly convex.	Two and one-half times as high as lateral wing of premaxillary; anteriorly convex.	Two times as high as lateral wing of premaxillary; straight.	One and one-half times as high as lateral wing of premaxillary; straight.	Two and one-half times as high as lateral wing of premaxillary; slightly convex anteriorly.
Nasals.....	Long, wide anteriorly, narrowing posteriorly; attached to ethmoid.	Long, widest posteriorly; attached to ethmoid.	Long, widest anteriorly and posteriorly, bearing posteromedial process; not attached to ethmoid.	Short, narrow, not attached to ethmoid.	Short, wide, bearing small posteromedial processes; not attached to ethmoid.	Moderately long narrowest anteriorly and posteriorly; not attached to ethmoid.
Ethmoid.....	Long; entirely ossified; smooth margins.	Long, entirely ossified; smooth margins.	Long, entirely ossified; smooth margins.	Short, about two-thirds ossified; irregular margins.	Moderately long; entirely ossified; smooth margins.	Short; one-half to entirely ossified; irregular margins.
Frontoparietal..	Small, ovid fontanelle present or absent; long, pointed postorbital processes curving along posterior border of orbit.	Large fontanelle, two and one-half times as long as wide; narrow supraorbital flanges with irregular margins.	Fontanelle absent; large supraorbital flanges having straight edges and extending posterolaterally.	Keyhole-shaped fontanelle; smooth margins; flanges absent.	Large, ovoid fontanelle; smooth margins; flanges absent.	Large, elongate fontanelle; smooth margins; flanges absent.
Squamosal.....	Large: anterior arm in contact with maxillary.	Large; anterior arm in contact with maxillary.	Large; anterior arm extending ½–⅔ way to maxillary.	Small; anterior arm extending ½ way to maxillary.	Moderately large; anterior arm extending ¼ way to maxillary.	Moderately small; anterior arm extending ¼–⅔ way to maxillary.

Within the *baudini* group, the skull of *S. cyanosticta* is the most generalized of the three species; the cranial characters are intermediate between *S. phaeota* and *S. baudini*. The lateral margins of the skull in *S. cyanosticta* are gently curved, and have an angularity anterior to the palatine-maxillary suture; the anterior margins are less angular in *S. phaeota*, which has a broader snout. Posteriorly in *S. baudini* the margins are slightly curved medially, and the greatest width of the skull is between the quadratojugal-maxillary sutures on either side of the skull. The frontoparietals of *S. cyanosticta* bear slightly irregular lateral margins and a large fontanelle. There is a tendency for obliteration of the fontanelle with increasing age in both *S. baudini* and *S. cyanosticta;* the lateral margins of the frontoparietals bear large supraorbital flanges in both of these species. In *S. phaeota* the flanges are most prominent; they extend posterolaterally with straight margins along two-thirds of the length of the orbit and terminate in rather blunt points. The broad interorbital flanges result in a relatively broad external interorbital distance. In *S. baudini* the flanges are curved posterolaterally around the orbit and terminate in sharp, thin points. The tegmen tympani of all three species are massive. In *S. cyanosticta* the proötics slope posteriorly, whereas they slope anteriorly in *S. baudini* and *S. phaeota.*

The skulls of *S. cyanosticta* and *S. baudini* are alike in certain respects. The squamosals of both species are large and connected to the maxillary by a bony connection; the squamosals of *S. phaeota* are large, but extend only two-thirds of the distance from the dorsal end of the quadrate to the maxillary. In *S. baudini* and *S. cyanosticta* the nasals are separated throughout their lengths from the ethmoid, whereas the nasals of *S. phaeota* are separated from the ethmoid by cartilage. The latter separation is due to an incomplete ossification of the nasals in *S. phaeota.* The bony part of each nasal is constricted in the middle of the long axis of the bone, and the nasals are widest anteriorly; posteriorly each nasal bears a medial process, which is narrowly separated from the lateral edge of the ethmoid.

The teeth of all species of *Smilisca* are spatulate and bifid. The numbers of maxillary, premaxillary, and vomerine teeth are summarized in Table 5. Smaller and presumably younger specimens of all species of *Smilisca* have fewer teeth than do larger specimens of the same species. This correlation

TABLE 5.—VARIATION IN THE NUMBER OF TEETH IN THE SPECIES OF SMILISCA. (ALL ARE MALES; N = NUMBER OF JAWS, OR TWICE THE NUMBER OF INDIVIDUALS; MEANS ARE GIVEN IN PARENTHESES AFTER THE OBSERVED RANGES.)

SPECIES	N	Maxillary	Premaxillary	Vomerine
S. baudini	20	49–65 (56.0)	9–16 (13.6)	5–9 (7.2)
S. cyanosticta	8	50–64 (57.9)	10–12 (10.8)	4–11 (7.1)
S. phaeota	20	50–68 (58.1)	10–15 (12.1)	5–9 (7.3)
S. puma	6	60–67 (63.6)	11–13 (12.0)	4–7 (5.3)
S. sila	8	48–60 (52.9)	10–14 (11.3)	5–7 (5.7)
S. sordida	12	39–55 (44.2)	7–11 (9.3)	4–6 (5.2)

between size and number of teeth does not exist as an interspecific trend within the genus; for example, the smallest species in the genus, *S. puma*, has the highest number of maxillary teeth. In small specimens of a given species wide gaps are present between the maxillary teeth posteriorly; in large specimens the gaps are filled by teeth, beginning anteriorly and progressing posteriorly, until the maxillary dentition is continuous.

Musculature

No extensive study of the muscular system was undertaken, but certain muscles know to be of taxonomic importance were studied.

Jaw Musculature.—Starrett (1960) pointed out the unique jaw musculature in *Smilisca*. In this genus M. depressor mandibulae consists of two parts, one arising from the dorsal fascia and one from the posterior arm of the squamosal. Two muscles arise from the anterior arm of the squamosal and insert on the lateral face of the mandible. Of these muscles, M. adductor mandibulae posterior subexternus lies medial to the mandibular branch of the trigeminal nerve; the other, M. adductor mandibulae externus superficialis, lies lateral to the same nerve (Fig. 9). In most other hylids the latter muscle is absent. No significant variation in the position of the muscles was noted in the various species of *Smilisca,* though M. adductor mandibulae originate somewhat more anteriorly in *S. baudini* and *S. cyanosticta* than in the other members of the genus, all of which have a shorter anterior arm of the squamosal that does not reach the maxillary. The two separate parts of M. depressor mandibulae are not so widely separated in members of the *sordida* group as in the *baudini* group.

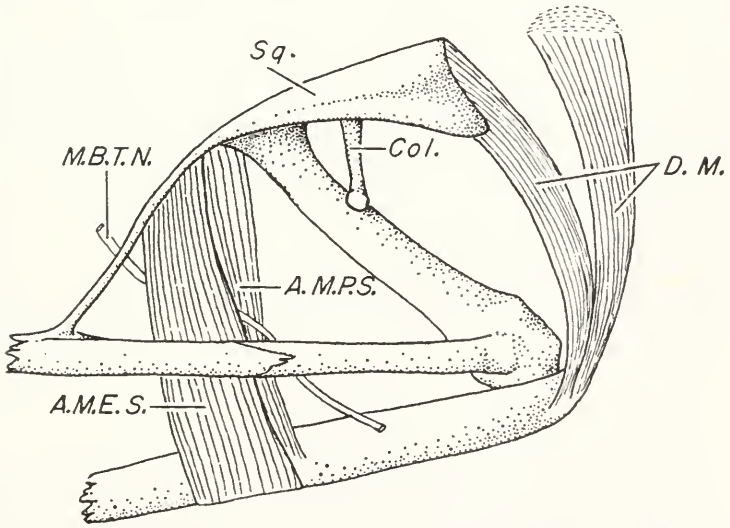


FIG. 9. Lateral view of the left jaw of *Smilisca baudini; A. M. E. S.*, adductor mandibulae externus superficialis; *A. M. P. S.*, adductor mandibulae posterior subexternus; *Col.*, columella; *D. M.* depressor mandibulae; *M. B. T. N.*, mandibular branch trigeminal nerve; *Sq.*, squamosal. KU 64214, ×5.

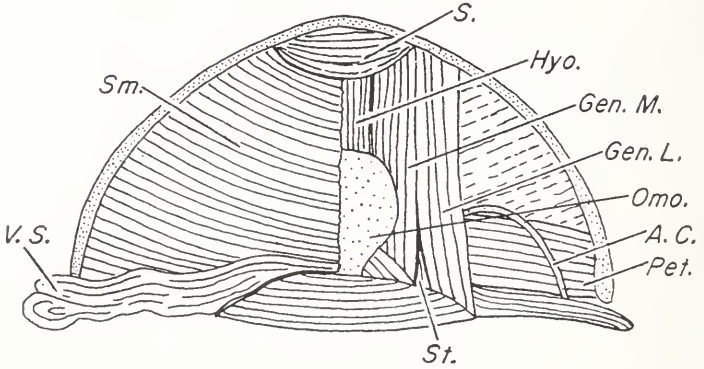


FIG. 10. Ventral view of throat musculature in an adult male *Smilisca baudini* (Superficial musculature on left, deep musculature on right); *A. C.* anterior cornua of hyoid; *Gen. L.*, geniohyoideus lateralis; *Gen. M.*, geniohyoideus medialis; *Hyo.*, hyoglossus; *Omo.*, omosternum; *Pet.*, petrohyoideus; *S.*, submentalis; *Sm.*, submaxillaris; *St.*, sternohyoideus; *V. S.*, vocal sac. KU 64220, ×2.5.

Throat Musculature.—The frogs that comprise the genus *Smilisca* are characterized by paired subgular vocal sacs, essentially the same as those in *Triprion* (Duellman and Klaas, 1964). The following description is based on *Smilisca baudini* (Fig. 10).

M. submentalis lies in the anterior angle of the lower jaw, is thick, and consists of transverse fibers extending between the dentaries. M. submaxillaris is thin and arises from the whole of the inner surface of the lower jaw, except for the anterior angle occupied by M. submentalis. Anteriorly M. submaxillaris is broadly attached by fascia to M. hyoglossus and M. geniohyoideus, which lie dorsal to M. submaxillaris. Medially this attachment continues posteriorly for about one-half the length of the hyoglossus. Posteriorly M. submaxillaris is folded and attached to M. sternoradialis of the pectoral girdle. The vocal sacs are formed by a pair of posterolateral evaginations of M. submaxillaris; a broad connection between the pouches allows free passage of air between the pouches.

The deeper throat musculature is essentially the same as that described for *Phrynohyas spilomma* by Duellman (1956), except for slight differences in the place of attachment on the hyoid.

SKIN

Structure

The skin of *Smilisca* is typical of that of most hylids in organization and structure. *Smilisca sila* is distinguished from other members of the genus by the presence of small wartlike protrusions and peculiar white, pustular spots on the dorsum. The wartlike structures are composed of three or four epidermal cells, which protrude from the surface of the epidermis; the structures are covered by a slightly thickened layer of keratin. The white pustules are slightly elevated above the surrounding skin. Internally they consist of ag-

gregations of swollen, granular, pigment-cells (perhaps lipophores) lying between the epidermis and the melanophores.

Biochemical Variations

Dried skins of all species of *Smilisca* were sent to José M. Cei, Instituto Nacional de Cuyo, Mendoza, Argentina, for biochemical screening by means of the chromatographic techniques described by Erspamer and Cei (1963). The species in the *baudini* group have detectable amounts of penta-hydroxi-trypatamine, whereas only a trace is present in the other species. Furthermore, species in the *baudini* group differ from *S. sila* and the *sordida* group in lacking, or having only a trace of, tryptophan-containing polypeptides. These superficial biochemical tests support the arrangement of species as ascertained by conventional taxonomic characters.

External Morphological Characters

The features of external morphology that were studied in connection with the taxonomy of the genus *Smilisca* are discussed below.

Size and Proportions

The frogs of the genus *Smilisca* are medium to large tree frogs. The three species comprising the *baudini* group (*S. baudini, cyanosticta,* and *phaeota*) are notably larger than *S. puma, sila,* and *sordida* (Table 6). The largest specimen that we examined is a female of *S. baudini* having a snout-vent length of 90 mm. *Smilisca puma* is the smallest species; the largest male has a snout-vent length of 38 mm. and the largest female, 46 mm.

No outstanding differences in proportions exist between species, although

TABLE 6.—COMPARISON OF SIZES AND CERTAIN PROPORTIONS OF THE SPECIES OF SMILISCA. (MEANS IN PARENTHESES BELOW OBSERVED RANGES; DATA FOR MALES ONLY.)

SPECIES	N	Snout-vent length	Tibia length/ snout-vent	Tympanum/ eye
S. baudini	140	47.3–75.9 (58.7)	42.1–53.6 (47.8)	56.1–94.4 (73.5)
S. cyanosticta	40	44.6–56.8 (50.7)	51.9–59.7 (56.0)	62.7–88.4 (71.4)
S. phaeota	50	40.8–65.5 (53.9)	50.9–60.2 (55.5)	62.7–85.5 (76.6)
S. puma	20	31.9–38.1 (34.7)	48.2–53.1 (51.3)	52.1–72.2 (64.9)
S. sila	33	31.6–44.8 (37.7)	49.7–58.1 (54.8)	47.6–58.3 (53.2)
S. sordida	55	31.9–44.6 (37.9)	50.5–57.1 (53.4)	46.5–57.1 (49.1)

certain proportions are sufficiently different in some species to warrant mention. *Smilisca baudini* is a more squat and stocky frog than other members of the genus; this is reflected in the somewhat shorter hind legs (Table 6). The size of the tympanum relative to that of the eye is highly variable within samples of a given species. Even so, noticeable differences in the tympanum/eye ratio are apparent. Members of the *baudini* group have the largest tympani, whereas *S. sila* and *sordida* have the smallest, and *S. puma* is intermediate (Table 6).

Shape of Snout

Although all members of the genus have rather truncate snouts, subtle differences exist among the species (Pl. 12). *Smilisca sila* has the shortest snout; that of *S. baudini* is only slightly longer. The snouts of *S. cyanosticta* and *puma* are nearly square in lateral profile, whereas those of *S. phaeota* and *sordida* are slightly inclined. The shape of the snout is relatively uniform within each species and displays no noticeable sexual dimorphism, except in *S. sordida,* in which there are sexual differences and geographic variation (see p. 324).

Hands and Feet

The characters of the hands and feet are among the most taxonomically important external features in *Smilisca.* Consistent differences exist in relative lengths of the digits, size of subarticular tubercles, size and number of supernumerary tubercles, size and shape of the inner metatarsal tubercle, and amount of webbing (Pls. 4 and 5). In the *baudini* group the series of species (*baudini-phaeota-cyanosticta*) show a progressive increase in amount of webbing in the hand and a decrease in number, and corresponding increase in size, of supernumerary tubercles. The amount of webbing in the feet of *S. baudini* and *phaeota* is about the same, but the webbing is slightly more extensive in *S. cyanosticta. Smilisca puma* is unique in the genus in lacking webbing in the hand; furthermore, this species is distinctive in having many large subarticular tubercles on the hand and a relatively small inner metatarsal tubercle. The two stream-inhabitants, *S. sila* and *sordida,* have shorter and stouter fingers than the other species. The webbing is most extensive in both the hands and feet of these species, which also are distinctive in having many small supernumerary tubercles on the feet.

Ontogenetic Changes

Minor ontogenetic changes in structure involve the shape of the snout, relative size of the eye, development of the tympanum, and amount of webbing in the hand. In recently metamorphosed young the snout is more rounded than in adults; the canthus and loreal concavity are not evident. Usually the tympanum is not differentiated in recently metamorphosed young, and the eye is proportionately large. The webbing in the feet is completely developed at metamorphosis, but young individuals have noticeably less webbing in the hand than do adults of the same species.

Coloration

Some of the most distinctive characters of the species of *Smilisca* are color and pattern of the living frogs. Although many chromatic features are lost or subdued in preserved specimens, the patterns usually persist.

Metachrosis

Change in color, well known in frogs, is common in hylids, especially in species having green dorsal surfaces (*Phyllomedusa* is a notable exception). The non-green *Smilisca* (*puma, sila,* and *sordida*) changes color, but this mostly is a change in intensity of color. In these species the markings usually are most distinct at night; frequently by day the frogs become pallid. The most striking examples of metachrosis in *Smilisca* are found in the *baudini* group, in which the dorsal ground-color changes from green to tan; correlated with the change in ground-color may be a corresponding change in the dorsal markings, but the dorsal markings may change to the opposite color.

Chromosomes

Chromosomes of all six species of *Smilisca* were studied by means of the propriono-orcein squash technique described by Duellman and Cole (1965). Karyotype analysis was attempted for several species by means of intraperitoneal injections of colchicine, which affected the mitotic cells as desired, but the testes examined contained too few mitotic cells to allow accurate determination of karyotypes.

Haploid (n) chromosome numbers were determined from cells in diakinesis, metaphase I, and metaphase II of meiosis. Diploid ($2n$) chromosome numbers were determined from cells in late prophase and metaphase of mitosis. Chromosome counts from as few as 23 meiotic cells of *S. phaeota* and as many as 80 cells of *S. sordida* reveal a constant haploid (n) number of 12; counts of chromosomes in one to five mitotic cells in all species, except *S. sila,* reveal that the diploid (2n) number is 24.

NATURAL HISTORY

Breeding

Like most hylid frogs *Smilisca* is most readily collected and observed when individuals congregate for breeding.

Time of Breeding

Smilisca breeds primarily in quiet water and reaches its height of breeding activity at times of plentiful rainfall,—usually from May through October. Through most of its range *Smilisca baudini* breeds in those months, but in some places where abundant rain falls in other seasons, the species breeds at those times. For example, in southern El Petén and northern Alta Verapaz, Guatemala, *Smilisca baudini* has been found breeding in February and March. The other pond-breeding species (*S. cyanosticta, phaeota,* and *puma*) live in regions lacking a prolonged dry season, and possibly they breed throughout the year, but breeding activity seems to be greatest in the rainiest months.

The two stream-breeding species (*S. sila* and *sordida*) breed in the dry season when the streams are low and clear, principally in December through April. At high elevations the species sometimes breed in the rainy season; also, individuals sometimes breed in the short dry season (summer canicula) in July and August.

At several localities species have been found breeding at different times of the year: *S. baudini* in March and July at Chinajá, Guatemala; *S. phaeota* in April and August at Palmar Sur, Costa Rica; *S. puma* in February and July at Puerto Viejo, Costa Rica; and *S. sila* in February, April, and August at El Volcan, Panamá. These observations indicate only that the population breeds at more than one time in the year, but do not provide any evidence on the breeding cycles of the individual frogs. This is one important aspect of the natural history of *Smilisca* for which we lack data.

Breeding Sites

All members of the genus *Smilisca* presumably deposit their eggs in water.

Smilisca baudini usually breeds in temporary rain pools; often these are nothing more than shallow, muddy puddles. In other instances the sites are extensive ditches or large flooded areas (Pl. 8, Fig. 1). This species is an opportunistic breeder, and males gather at any of a wide variety of suitable breeding sites that are formed by torrential rains in the early part of the rainy season. *Smilisca baudini* nearly always breeds in open pools having bare earthen edges. Frequently congregations of *S. baudini* are found at such small pools, but are absent from nearby large ponds surrounded by vegetation.

Little is known of the breeding habits of *S. cyanosticta,* which inhabits humid forests on foothills and lowlands. Apparently its breeding sites are not unlike those of *S. phaeota,* which usually are pools surrounded by vegetation (Pl. 8, Fig. 2), although sometimes males of *S. cyanosticta* call from open muddy puddles. In uplands, where standing water is uncommon, this species breeds in quiet pools in streams.

Smilisca puma breeds in grass-choked ponds and marshes, where the males call from bases of dense clumps of grass in the water (Pl. 9, Fig. 1).

Smilisca sila and *S. sordida* differ noticably from other species in the genus by breeding exclusively in streams, where males usually call from rocks or gravel bars in or at the edges of streams (Pl. 9, Fig. 2); sometimes individuals perch on bushes overhanging streams. In the streams, or parts of streams, utilized by these frogs the water is clear, shallow, and has a slow gradient; occasional males have been found calling along cascading mountain streams.

Breeding choruses composed of ten or more species of frogs are not uncommon in Middle America, but *Smilisca* usually breeds alone or with one or two other species and at the most five others. This tendency towards solitary breeding possibly is the result of selection of breeding sites that are unsuitable to many other species of frogs. Nevertheless, many other species of frogs have been found at the breeding sites with the various species of *Smilisca;* these breeding associates (Table 7) are most numerous for *S. baudini,* which has a broad geographic range, including a variety of habitats.

Breeding Behavior

Calling sites.—All species of *Smilisca* usually call from the ground, including rocks and gravel bars; some individuals sit in shallow water near the edge of the pool or stream. Sometimes males of *S. baudini, sila,* and *sordida* call from low bushes or trees near the breeding site. One *S. baudini* was observed calling while it was floating on the surface of a pond. *Smilisca cyanosticta, phaeota,* and *puma* call from secluded places at the edge of the water or in the water, whereas *S. baudini, sila* and *sordida* call from open situations.

TABLE 7.—BREEDING ASSOCIATES OF THE VARIOUS SPECIES OF SMILISCA.

ASSOCIATE	*S. baudini*	*S. cyanosticta*	*S. phaeota*	*S. puma*	*S. sila*	*S. sordida*
Rhinophrynus dorsalis	X	—	—	—	—	—
Leptodactylus bolivianus	—	—	X	—	—	—
Leptodactylus labialis	X	—	X	—	—	—
Leptodactylus melanonotus	X	—	X	X	X	—
Leptodactylus occidentalis	X	—	—	—	—	—
Leptodactylus quadrivittatus	—	—	X	—	—	—
Leptodactylus pentadactylus	—	—	X	X	—	X
Engystomops pustulosus	X	—	X	—	—	—
Bufo canaliferus	X	—	—	—	—	—
Bufo cavifrons	—	X	—	—	—	—
Bufo coccifer	X	—	—	—	—	—
Bufo coniferus	—	—	X	—	—	—
Bufo cristatus	—	X	—	—	—	—
Bufo gemmifer	X	—	—	—	—	—
Bufo haematiticus	—	—	X	—	X	X
Bufo kellogi	X	—	—	—	—	—
Bufo luetkeni	X	—	—	—	—	—
Bufo marinus	X	—	X	X	X	X
Bufo marmoreus	X	—	—	—	—	—
Bufo mazatlanensis	X	—	—	—	—	—
Bufo melanochloris	—	—	X	—	X	X
Bufo perplexus	X	—	—	—	—	—
Bufo typhonius	—	—	X	—	X	—
Atelopus varius	—	—	—	—	X	X
Diaglena reticulata	X	—	—	—	—	—
Diaglena spatulata	X	—	—	—	—	—

TABLE 7.—*Continued*

ASSOCIATE	*S. baudini*	*S. cyanosticta*	*S. phaeota*	*S. puma*	*S. sila*	*S. sordida*
Hyla boulengeri	—	—	X	—	—	—
Hyla colymba	—	—	—	—	X	—
Hyla ebraccata	X	—	X	—	—	—
Hyla elaeochroa	—	—	X	X	—	—
Hyla eximia	X	—	—	—	—	—
Hyla legleri	—	—	—	—	—	X
Hyla microcephala	X	—	X	—	—	—
Hyla phlebodes	—	—	X	X	—	—
Hyla picta	X	—	—	—	—	—
Hyla robertmertensi	X	—	—	—	—	—
Hyla rosenbergi	—	—	X	—	—	—
Hyla rufioculis	—	—	—	—	—	X
Hyla smithi	X	—	—	—	—	—
Hyla staufferi	X	—	—	—	—	—
Hyla walkeri	X	—	—	—	—	—
Phrynohyas inflata	X	—	—	—	—	—
Phrynohyas spilomma	X	—	—	—	—	—
Phrynohyas venulosa	X	—	—	—	—	—
Phyllomedusa callidryas	X	—	X	—	—	—
Phyllomedusa dacnicolor	X	—	—	—	—	—
Phyllomedusa moreleti	X	X	—	—	—	—
Pternohyla fodiens	X	—	—	—	—	—
Smilisca baudini	X	X	—	—	—	—
Smilisca cyanosticta	X	X	—	—	—	—
Smilisca phaeota	—	—	X	—	—	—
Smilisca puma	—	—	—	X	—	—

TABLE 7.—*Concluded*

ASSOCIATE	*S. baudini*	*S. cyanosticta*	*S. phaeota*	*S. puma*	*S. sila*	*S. sordida*
Smilisca sila	—	—	—	—	X	X
Smilisca sordida	—	—	X	—	X	X
Triprion petasatus	X	—	—	—	—	—
Cochranella fleischmanni	—	—	—	—	X	X
Centrolene prosoblepon	—	—	—	—	X	—
Gastrophryne elegans	X	—	—	—	—	—
Gastrophryne olivacea	X	—	—	—	—	—
Gastrophryne usta	X	—	—	—	—	—
Hypopachus alboventer	X	—	—	—	—	—
Hypopachus caprimimus	X	—	—	—	—	—
Hypopachus inguinalis	X	—	—	—	—	—
Hypopachus maculatus	X	—	—	—	—	—
Hypopachus oxyrrhinus	X	—	—	—	—	—
Hypopachus variolosus	X	—	—	—	—	—
Rana palmipes	X	—	X	X	—	—
Rana pipiens	X	—	—	—	—	—
Rana warschewitschi	—	—	X	—	X	X

Chorus structure.—Limited observations on some of the species of *Smilisca* show a definite organization of the calling behavior of individuals. *Smilisca baudini* and *S. phaeota* call in duets. This is especially noticeable in *S. baudini*, in which the members of a duet often call from sites separated by only a few centimeters. The call of *S. baudini* consists of a series of like notes (see description of call in following section); the duration of each note is about equal to the interval between notes. Normally one individual utters one note, pauses, and utters a single note again, or series of two or three notes. If there is no response, the first individual often waits several seconds or even several minutes and then repeats the call. The second individual usually responds after the first or second note of the sequence. The notes of the second individual usually are spaced so that they are emitted in the intervals between the notes of the first individual. This can be shown diagrammatically by having

the figure "1" represent notes of the first individual and figure "2," the notes of the second; an empty interval is represented by "0":

1–0–1–2–1–2–1–2–1–2–1–2

Usually a chorus is initiated by one duet and is quickly picked up by other individuals also calling in duets. A numerical representation of a chorus of eight frogs would approximate the following organization:

1–0–1–2–1–2–1–2–1–2–1–2–1–2
3–0–3–4–3–4–3–4–3–4–3–4–3
5–6–5–6–5–6–5–6–5–6–5–6
7–8–7–8–7–8–7–8–7–8–7–8

After the first one or two duets are initiated, the second individuals in the following duets usually call immediately after their respective partners have given the first notes. The other noteworthy aspect about the organization is that the entire chorus usually stops abruptly. Normally the first duet stops calling shortly before the others, but this is not invariable. Often one duet or one individual will emit several notes after the rest of the frogs have become silent. An interval of several minutes sometimes elapses before the chorus begins again. Successive choruses apparently are initiated by the same duet. Responses can be initiated artificially by imitating the call, and sometimes any loud noise will start a chorus.

Similar duets have been observed in *S. phaeota*. In this species the intervals are often much longer than the notes, and if two males are calling in close proximity, their calls can be mistaken for those of one individual. *Smilisca phaeota* does not congregate in large numbers; usually only two males call from one restricted site.

Smilisca sila has a call consisting of a primary note followed by one or more secondary notes. Males often call in duets, but not necessarily so. In a duet, the first male usually utters only primary notes until the second individual responds; then each individual produces a rapid series of secondary notes.

Smilisca puma also produces primary and secondary notes. Although individuals sometimes call alone, duets, trios, or quartets were more common. The chorus is initiated by one individual uttering primary notes until joined by the second, third, and fourth frogs. In one quartet in a marsh 7.5 kilometers west of Puerto Viejo, Costa Rica, on February 19, 1965, the same individual initiated four consecutive choruses. Each time the second member of the chorus was the same; the third and fourth frogs joined the chorus nearly simultaneously.

Individuals of *S. sordida* are usually irregularly situated along a stream. No duets or other combinations of individuals are apparent in the chorus structure, but once an individual calls, a frog nearby calls almost immediately; then a frog near the second individual calls, and so on. The resulting series of calls gives the impression that the sound is moving along the stream as successive individuals join the chorus and the first callers become quiet. It is not known if the same individual initiates successive choruses or if the order of calling is the same in subsequent choruses.

These limited observations on chorus structure in *Smilisca* show the presence of behavioral organization. The methods of establishing the organization and the significance of the call-order in breeding have yet to be discovered.

Calling males of *S. baudini* are often close together; some individuals have been observed almost touching one another, but no indication of territoriality

or aggressive behavior has been witnessed. The more distant spacing of the stream-breeding species *S. sila* and *S. sordida* may be a function of calling-territories, but no direct evidence is available to substantiate this supposition.

Sex recognition and amplexus.—Observations on *Smilisca baudini* indicate that the calls of males attract females. At Tehuantepec, Oaxaca, México, a female was first observed about two meters away from a male calling at the edge of a rain pool; in a series of short hops she progressed directly towards the male, although vegetation obscured him until she was less than a meter away. When she approached to within about 20 centimeters of the male, he took notice of her, moved to her, and clasped her. At Chinajá, Alta Verapaz, Guatemala, a female swam directly across a pool about three meters wide to a calling male. Her line of movement took her within a few centimeters of a silent male, to whom she paid no attention. She stopped just in front of the calling male, which immediately clasped her. At a large muddy pond 4 kilometers west-northwest of Esparta, Puntarenas, Costa Rica, a female was observed swimming toward a small submerged tree; a male was calling from a branch about one meter above the water. The female climbed to a branch about 20 centimeters below the male, which upon seeing her there immediately jumped down and clasped her. These few observations of *S. baudini* show that in this species females are capable of locating calling males by means of phono-orientation; visual reception on the part of females seems to be secondary. Contrariwise, males apparently become aware of the proximity of females by seeing them; once a male sees a female he usually tries to clasp her. Possibly the males receive stimuli by means of chemoreception, but in each observed instance the male obviously looked at the female.

Amplexus is axillary in all members of the genus. Normally amplexing males hunch their backs and press their chins to the females' backs. Clasping pairs are usually found at the edge of the water, but sometimes amplexus takes place in trees or bushes.

Egg deposition.—Oviposition has been observed only in *Smilisca baudini*. On the night of June 28, 1961, at Chinajá, Alta Verapaz, Guatemala, a clasping pair was observed at the edge of a shallow rain pool. After sitting for several minutes in shallow water, the female (with male on her back) swam part way across the pool and grasped an emergent stick with one hand. The female's body was nearly level with the surface of the water, and her hind legs were outstretched as deposition commenced; eggs were extruded rapidly. After a few seconds the female moved slowly to another twig a few centimeters away and deposited more eggs. This process was repeated until the female was spent. The spawn resulted in a surface film covering roughly one square meter. It is doubtful if this type of egg deposition occurs in any other species in the genus, especially those that lay their eggs in streams.

Breeding Call

The breeding calls of the six species of *Smilisca* are alike in their explosive nature. Calls are emitted quickly with a short burst of air filling the vocal sac, which immediately deflates. Phonetically the calls can be described as a single "wonk" or series of such notes in *S. baudini* and *S. cyanosticta*, a low growl in *S. phaeota*, a relatively high pitched rattle in *S. sordida*, and a low

Table 8.—Comparison of Breeding Calls in Smilisca. (Observed Range Given in Parentheses Below Mean. In Species Having Primary and Secondary Notes, Only the Primary Notes Are Analyzed Here.)

Species	N	Notes per call group	Duration of note (seconds)	Pulses per second	Fundamental frequency (cps)	Major frequencies (cps)	
						Lower	Upper
S. baudini	20	8.0 (2–15)	0.11 (0.09–0.13)	174.7 (140–195)	166.2 (135–190)	351 (175–495)	2507 (2400–2725)
S. cyanosticta	10	1.2 (1–2)	0.38 (0.25–0.45)	147.0 (110–180)	145.1 (135–160)	841 (480–975)	1894 (1600–2100)
S. phaeota	10	1.6 (1–2)	0.31 (0.10–0.45)	116.0 (100–130)	143.0 (110–165)	372 (330–495)	.....
S. puma	28	3.7 (2–10)	0.13 (0.06–0.35)	208.2 (187–240)	145.6 (125–200)	743 (495–980)	1868 (1456–2240)
S. sila	15	2.4 (1–6)	0.16 (0.06–0.28)	108.5 (97–120)	103.0 (90–115)	899 (665–1180)	2218 (1980–2700)
S. sordida	19	1.7 (1–6)	0.29 (0.18–0.45)	104 7 (78–135)	123.1 (90–140)	1216 (1150–1540)	2694 (2340–2990)

squawk usually followed by one or more rattling secondary notes in *S. puma* and *S. sila*. Quantitatively, the calls of the six species differ in number of notes, duration of notes, and in pitch (Table 8, Pls. 10 and 11). Although no measurements were taken on the intensity of the calls, we observed in the field that each of the species has a loud voice. The call of *S. baudini* seems to carry farther than any of the others.

Call rate.—The rate at which call-groups are produced varies from one every few seconds to one in several minutes. In *S. baudini, cyanosticta, phaeota,* and *sordida,* call-groups are produced as frequently as every 12 seconds, but usually more time elapses between call groups. In *S. sordida,* five or more minutes sometimes elapse between call-groups. The interval is somewhat less in *S. phaeota.* Calls are repeated at much shorter intervals in *S. puma* (5-55 seconds) and *S. sila* (4-20 seconds).

Notes per call-group.—Except for *S. puma* and *S. sila,* the series of notes produced in any given call of a species of *Smilisca* is essentially the same; there is no differentiation into primary and secondary notes. *Smilisca cyanosticta* and *S. phaeota* emit only one or two relatively long notes per call-group, whereas *S. baudini* and *S. sordida* produce as many as 15 and 6 notes, respectively. Males of *S. puma* and *S. sila* often produce only the primary note; sometimes this is done several times before the secondary notes are produced. For example, one *S. puma* (KU 91711; tape No. 379) produced the following number of notes in consecutive call-groups: 1, 1, 1, 1, 2, 2, 3, 1, 4; secondary notes are present in only four of the nine call-groups. A typical series of consecutive call-groups in *S. sila* (KU 91852; Tape No. 385) has 1, 1, 1, 2, 4, 2 notes per call-group; secondary notes are present in only half of the call-groups. *Smilisca puma* apparently always produces at least two primary notes before emitting secondary notes; sometimes only primary notes are produced in one series of calls. The number of secondary notes following a given primary varies from one to nine; the modal number is one, and the mean is three in 27 call-groups. *Smilisca sila* frequently begins a series of calls with two or more primary notes, but sometimes the first primary note is followed immediately by two or more secondary notes. The number of secondary notes following a given primary varies from one to five; the modal number is one, and the average is two in 13 call-groups.

Duration.—The average duration of call-groups consisting of two or more notes is 1.18 seconds in *S. baudini;* 1.02 in *cyanosticta,* 0.91 in *phaeota,* 1.32 in *puma,* 1.48 in *sila,* and 1.29 in *sordida.* Although there is considerable variation in the lengths of the notes (only primary notes in *S. puma* and *sila* are considered here), *S. cyanosticta, phaeota,* and *sordida* have noticeably longer notes than do the other species (Table 8). The secondary notes are longer than the primary notes in *S. puma* (average 0.27 secs. as compared with 0.13 secs.) and in *S. sila* (average 0.25 secs., as compared with 0.16 secs.).

Note repetition rate.—The rate at which notes in call-groups containing two or more notes are produced varies in *S. baudini* from 2.5 to 7.1 (average, 3.7) calls per second; *cyanosticta,* 1.8-2.1 (1.9); *phaeota,* 2.0-2.4 (2.2); *puma,* 1.9-2.9 (2.2); *sila,* 1.3-2.4 (1.8); and *sordida,* 1.5-2.6 (2.1). *Smilisca baudini,* which has notes of short duration (0.09 to 0.13 seconds), has the fastest note-repetition rate. Although the individual notes of *S. cyanosticta* and *S. phaeota* are relatively long (average, 0.38 and 0.31 seconds, respectively), the intervals

between the notes is short; consequently, their note-repetition rates do not differ greatly from those of *S. puma* and *S. sila,* which have shorter notes (average, 0.13 and 0.16 seconds, respectively) but longer intervals between notes.

Pulse rate.—Pulses vary in frequency from 78 to 240 per second in the calls analyzed (only primary notes in *S. puma* and *S. sila*), but the variation in any given species is much less than that in the entire genus (Table 8). *Smilisca puma* is outstanding in having a high pulse rate, which is approached only by that of *S. baudini.* Even in the species having the lowest pulse rates, the pulsations are not audible. The secondary notes produced by *S. puma* and *S. sila* have a slower pulse rate than the primary notes; often the pulses are audible. In *S. puma* the pulse rate of secondary notes is sometimes as low as 48 pulses per second, and in *S. sila* still lower (as low as 40 pulses per second). The upper limits of pulse rate in the secondary notes in these species merge imperceptibly with the rates of the primary note; consequently, on the basis of pulse rate alone it is not always possible to distinguish primary from secondary notes.

Frequency.—*Smilisca* produces noisy (as opposed to more musical) calls, and the energy is distributed throughout the frequency spectrum; the calls are poorly modulated, except in *S. sordida,* in which two usually discrete bands of frequency are present (Pl. 11C). For the most part the calls of *Smilisca* consist of little modified energy of the fundamental frequency and of its harmonics, some of which are emphasized.

The upper frequency range varies within each species and even within the calls of one individual. *Smilisca phaeota* has the lowest upper frequencies; no calls ranged above 4400 cycles per second (cps.), and half of the calls never exceeded 3000 cps. *Smilisca cyanosticta* produces calls in which the upper frequency is below 7000 cps. and usually below 6000 cps. Likewise, *S. puma* produces calls that are below 7000 cps., whereas *S. sila* has frequencies of up to 8400 cps. In both *S. baudini* and *S. sordida,* the highest frequencies attained are about 9100 cps. Variation in the highest frequencies in a series of consecutive calls by one individual frog was noted in all species. Such variation is especially prevalent in *S. puma;* for example one individual (KU 87771; Tape No. 376) recorded at a temperature of 24° C. at 7.5 kilometers west of Puerto Viejo, Heredia Province, Costa Rica, on July 31, 1964, produced three consecutive primary notes having upper frequencies of about 6000, 4000, and 4000 cps., respectively. Apparently in a given species the production of the higher frequencies in some notes and not in others is correlated with the amount of distention of the vocal sac and is not dependent upon the structure or tension of the vocal cords.

Although the dominant frequency in *S. sordida* is lower than that in *S. baudini* and *S. cyanosticta,* the call of the former is audibly higher-pitched. This is due primarily to the emphasis on certain harmonics at a high frequency (sometimes as high as 9000 cps.) in *S. sordida,* whereas in *S. baudini* and other species, if harmonics are present at those frequencies, they are not emphasized.

The fundamental frequencies are as low as 90 cps. in *S. sila* and *S. sordida* and as high as 200 cps. in *S. puma* (Table 8). The fundamental frequency seemingly is relatively unimportant in determining the general pitch of the call, a characteristic most dependent on the dominant frequency and emphasized harmonics in the higher-frequency spectrum. In none of the species is the

fundamental the dominant frequency. In the low-pitched call of *S. phaeota* the dominant frequency is the third harmonic (the second harmonic above the fundamental frequency, which is the first harmonic). In all other species a much higher harmonic is dominant; for examples, in *S. cyanosticta* harmonics from 10 to 15 are dominant; in *S. baudini*, 15-19; and *S. sila*, 20-30.

A glance at the audiospectrographs and their accompanying sections (Pls. 10 and 11) reveals the presence of two emphasized bands of frequency in all species except *S. phaeota*, in which only the lower band is present. These two bands of emphasized harmonics are part of a continuous, or nearly continuous, spread of energy throughout the frequency spectrum, except in *S. sordida* in which the bands are usually distinct. As shown in the sections, certain harmonics in each of the bands are emphasized with nearly equal intensity. Therefore, with the exception of *S. phaeota*, the calls of *Smilisca* are characterized by two major frequencies, one of which is the dominant frequency and the other is a subdominant frequency (Table 8). The upper major frequency is dominant in all calls in *S. baudini* and *S. cyanosticta*, but either major frequency may be dominant in other species. The upper major frequency is dominant in 65 per cent of calls by *S. puma*, 87 per cent in *S. sila*, and 68 per cent in *S. sordida*. Individuals of these three species sometimes produce a series of calls in which the dominant frequency changes from one of the major frequencies to the other. Four consecutive notes emitted by an individual of *S. sordida* recorded 13 kilometers east-northeast of Golfito, Puntarenas Province, Costa Rica, had dominant frequencies of 910, 1950, and 750 cps., respectively. In each case, an alternation of major frequencies took place in respect to dominance. An individual of *S. puma* from 7.5 kilometers west of Puerto Viejo, Costa Rica, produced a primary note followed by one secondary note; each note had major frequencies at 600 and 1800 cps.; the dominant frequency of the primary note was at 1800 cps., whereas in the secondary note the dominant frequency was at 600 cps. The difference in emphasis on the major frequencies is so slight that shift in dominance is not audible.

Effect of temperature on calls.—The present data are insufficient to test statistically the correlation between temperature and variation within certain components of the calls in *Smilisca*, but even a crude graph shows some general correlations. The widest range of temperatures is associated with the recordings of *S. baudini*. Three individuals recorded at a temperature of 30° C. at Tehuantepec, Oaxaca, had pulse rates of 180 pulses per second and fundamental frequencies of 160-180 cps., as compared with an individual recorded at a temperature of 17° C., which had a pulse rate of 140 and a fundamental frequency of 135 cps. All individuals of *S. baudini* recorded at higher temperatures had faster pulse rates and higher fundamental frequencies. Pulse rates differ in the other species in the genus but less strikingly (probably owing to narrower ranges of temperatures at which recordings were made). In five recordings of *S. sordida* made at 20° C. the pulse rate is 80-90, as compared with four recordings made at 25° C. having pulse rates of 120-135. Thirteen recordings of *S. sila* made at 17° C. have pulse rates of 97-112 (average 105); one individual recorded at 26° C. has 120 pulses per second. Seemingly no correlation exists between temperature and other characteristics of the calls, such as duration and rate of note-repetition.

The breeding call as an isolating mechanism.—Blair (1958), Bogert (1960), Duellman (1963a), Fouquett (1960), Johnson (1959), and others have pro-

vided evidence that the breeding calls of male hylids (and other anurans) serve as isolating mechanisms in sympatric species. In summarizing this discussion of the breeding calls of *Smilisca* we want to point out what seem to be important differences in the calls that may prevent interspecific hybridization in sympatric species of *Smilisca.*

The genus is readily divided into two species-groups on morphological characters; this division is supported by the breeding calls. In the species of the *baudini* group the calls are unmodulated and lack secondary notes. In the *sordida* group the calls either have secondary notes or are modulated.

Smilisca baudini occurs sympatrically with *S. cyanosticta* and *S. phaeota;* where they occur together, both species sometimes breed in like places at the same time. We are not aware of these species breeding synchronously at exactly the same site, although *S. baudini* and *S. cyanosticta* were calling on the same nights and less than 100 meters apart in Oaxaca in June, 1964. Regardless of their respective breeding habits, sympatric species have calls that differ notably. Except for the higher fundamental and dominant frequencies, the calls of *S. cyanosticta* and *S. phaeota* closely resemble one another, but the calls of both species differ markedly from that of *S. baudini.* The geographic ranges of *S. cyanosticta* and *S. phaeota* are widely separated.

The calls of the allopatric species *S. puma* and *S. sila* are not greatly different. *Smilisca sordida* has a distinctive call and occurs sympatrically with *S. puma* and *S. sila.* In the streams in southern Costa Rica *S. sordida* and *S. sila* breed synchronously, but the high-pitched modulated call of the former is notably different from the lower, unmodulated call of *S. sila.*

The data indicate that the calls of related sympatric species differ more than the calls of related allopatric species. We postulate that these differences evolved to support the reproductive isolation of the sympatric species. The data are insufficient to determine geographic variation in the calls and to determine if differences in the calls are enhanced in areas of sympatry as compared with the allopatric parts of the ranges.

Other calls.—As stated previously, there is no direct evidence of territoriality in *Smilisca;* we have heard no calls that can be definitely identified as territorial. Single notes of *S. baudini, phaeota,* and *sila* have been heard by day, just prior to rains, or during, or immediately after rains. Such calls can be interpreted as "rain calls," which are well known in *Hyla eximia* and *Hyla squirella.* Distress calls are known in several species of *Rana* and in *Leptodactylus pentadactylus;* such calls result from the rapid expulsion of air over the vocal cords and with the mouth open. Distress calls have been heard from *S. baudini.* At Charapendo, Michoacán, México, a male that had one hind limb engulfed by a *Leptodeira maculata* emitted several long, high-pitched cries. A clasping pair of *S. baudini* was found in a bush at the edge of a marshy stream 2 kilometers northeast of Las Cañas, Guanacaste Province, Costa Rica. When the pair was grasped, the female emitted a distress call.

Eggs

Eggs of *S. baudini, cyanosticta,* and *phaeota* have been found in the field, and eggs of *S. sila* have been observed in the laboratory. The eggs of *S. puma* and *sordida* are unknown. Insofar as known, *Smilisca baudini* is unique in the genus in depositing the eggs in a surface film. Each egg is encased in a

vitelline membrane, but individual outer envelopes are lacking. The eggs are small; the diameter of recently-deposited eggs is about 1.3 mm. and that of the vitelline membrane is about 1.5 mm. The eggs of *S. cyanosticta* and *phaeota* are deposited in clumps, and the eggs are larger than those of *S. baudini*. Diameters of eggs of *S. cyanosticta* are about 2.3 mm., and those of the outer envelopes are about 4.0 mm. Artificially fertilized eggs of *S. sila* raised in the laboratory have diameters of about 2.4 mm.; the diameter of the outer envelopes is about 4.9 mm.

In order to determine the reproductive potential of the six species, ovulated eggs were removed from females and counted. The numbers of eggs recorded are: 3 *S. baudini*—2620, 2940, 3320; 1 *S. cyanosticta*—910; 3 *S. phaeota*—1665, 1870, 2010; 1 *S. puma*—518; 3 *S. sila*—369, 390, 473; 3 *S. sordida*—524, 702, 856. These limited data indicate that the large species (*S. baudini, cyanosticta,* and *phaeota*) have more eggs than do the smaller species. The stream-breeding species (*S. sila and sordida*) have relatively few eggs by comparison with the pond-breeders. Possibly this is a function of size of eggs rather than a correlation with the site of egg-deposition.

Tadpoles

The acquisition of tadpoles of all of the species of *Smilisca* has made possible the use of larval characters in erecting a classification and in estimating the phylogenetic relations of the several species. Furthermore, developmental series of tadpoles of four species allow a comparison of the growth and development in these species. Throughout the discussion of tadpoles we have referred to the various developmental stages by the Stage Numbers proposed by Gosner (1960).

General Structure

Tadpoles of the genus *Smilisca* are of a generalized hylid type, having ⅗ tooth-rows, unspecialized beaks, mouth partly or completely bordered by papillae, lateral fold present in the lips, spiracle sinistral, anal tube dextral, and caudal musculature extending nearly to tip of caudal fin. Although minor differences exist in coloration, proportions, and mouthparts, no great modifications of the basic structure are present.

Comparison of Species

The larval characters of the species of *Smilisca* are compared below and illustrated in Figures 11-15.

Shape and Proportions.—The bodies of *S. baudini, cyanosticta, phaeota,* and *puma* are rounded and about as wide as deep; the eyes are moderately large and directed dorsolaterally, and the nostrils are about midway between the bluntly rounded snout and the eyes. The mouths are medium-sized and directed anteroventrally. The bodies of tadpoles of *S. sila* and *sordida* are slightly compressed dorso-ventrally. The snout is moderately long and sloping; the eyes are larger and directed more dorsally than in the other species, and the nostrils are closer to the eyes than the snout. The mouths are moderately large and directed ventrally.

The tail is about half again as long as the body in *S. baudini, cyanosticta,*

phaeota, and *puma;* in these species the caudal musculature is moderately heavy, and the caudal fins are deep. The caudal musculature is upturned distally in *S. baudini* and *phaeota,* and the dorsal fin extends anteriorly onto the body in these two species and in *S. puma.* The tail is about twice as long as the body in *S. sila* and *sordida.* In both species the caudal fins are shallow in comparison with the depth of the caudal musculature, especially in *S. sordida* (Fig. 14); in neither species does the dorsal fin extend anteriorly onto the body.

Mouthparts.—The mouth of *S. sordida* is completely bordered by two rows of papillae, whereas in the other species the median part of the upper lip is devoid of papillae. *Smilisca baudini* and *puma* have two rows of papillae; *S. sila* has one complete row (except medially on the upper lip) and one incomplete row, and *S. cyanosticta* and *phaeota* have only one row (Fig. 15). All species have numerous papillae in the lateral fold; the fewest lateral papillae

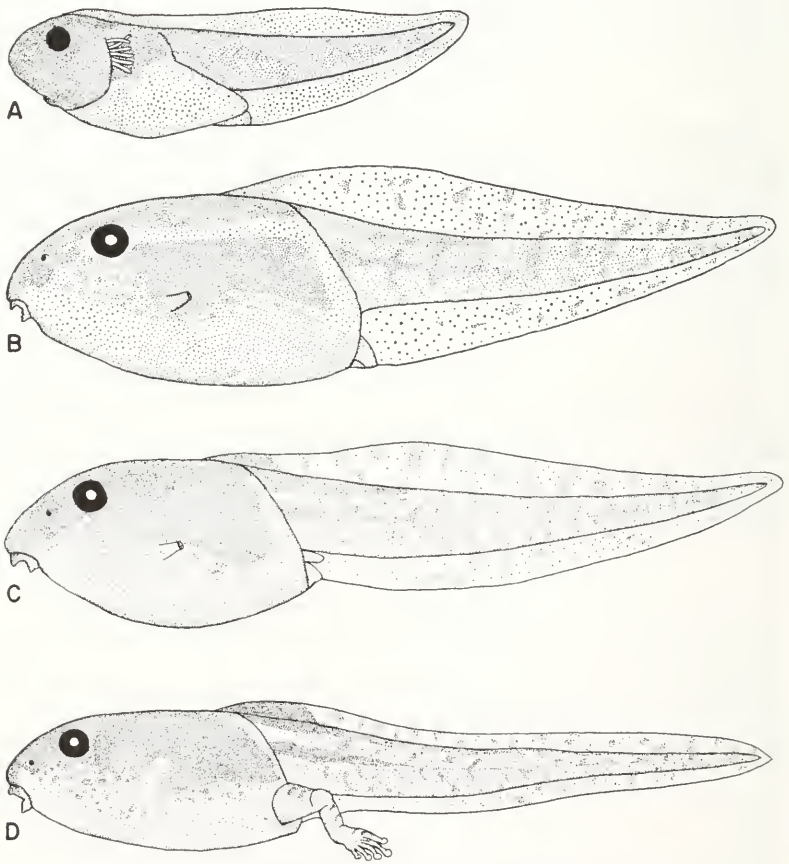


Fig. 11. Tadpoles of *Smilisca baudini:* (A) Stage 21 (KU 62155) ×10; (B) Stage 25 (KU 68467) ×5; (C) Stage 30 (KU 60018) ×4; (D) Stage 41 (KU 60018) ×3.

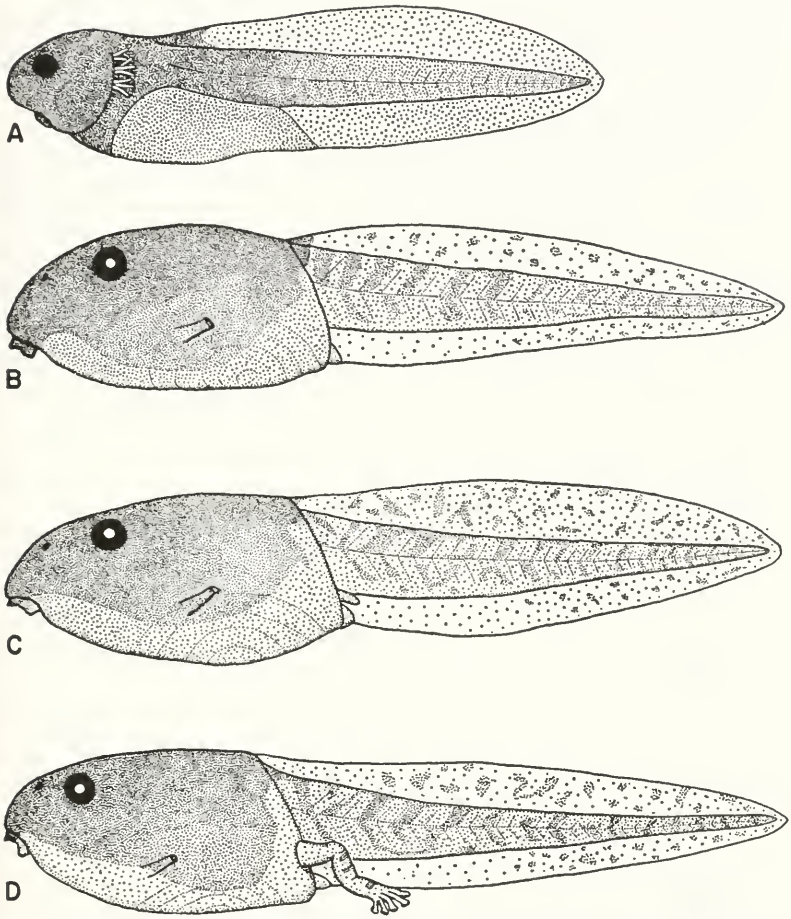


FIG. 12. Tadpoles of *Smilisca cyanosticta:* (A) Stage 21 (KU 87648) (B) Stage 25 (KU 87651) ×5; (C) Stage 30 (KU 87652) ×4; (D) Stage 40 (KU 87650) ×3.

are found in S. *cyanosticta* and *phaeota.* Although all species have two rows of teeth in the upper jaw and three rows in the lower jaw, specific differences in the nature of the rows exist between certain species. The second upper tooth-row is narrowly interrupted medially in S. *sila* and *sordida* and broadly interrupted in the other species. The first upper row is strongly arched in S. *puma,* moderately arched in S. *baudini* and *sila,* and weakly arched in the other species. In all species the third lower tooth-row is the shortest, only slightly so in S. *sila* and *sordida,* but only about half the length of the second lower row in S. *puma.*

The beaks are well developed and finely serrate in all species. The lower, broadly V-shaped, beak is slender in S. *puma,* rather robust in S. *baudini* and

sila, and moderately heavy in the other species. The lateral processes of the upper beak are shortest in *S. puma* and longest in *S. baudini* and *sordida.* In the latter the inner margin of the upper beak and lateral process have the form of a shallow S, whereas in the other species the inner margin of the upper beak forms a continuous arch with the lateral processes (Fig. 15).

Coloration.—The tadpoles of *Smilisca* lack the bright colors or bold markings characteristic of some hylid tadpoles; even so, the subdued colors and arrangement of pigments provide some distinctive markings by which the species can be distinguished from one another. The species comprising the *baudini* group (*S. baudini, cyanosticta,* and *phaeota*) are alike in having the body brown or grayish brown dorsally and transparent with scattered brown pigment ventrally. A cream-colored, crescent-shaped mark is present on the posterior edge of the body; this mark is usually most noticeable in *S. baudini* and least so in *S. cyanosticta.* Other differences in coloration in members of the *baudini* group are relative and subtle. *Smilisca phaeota* usually is more

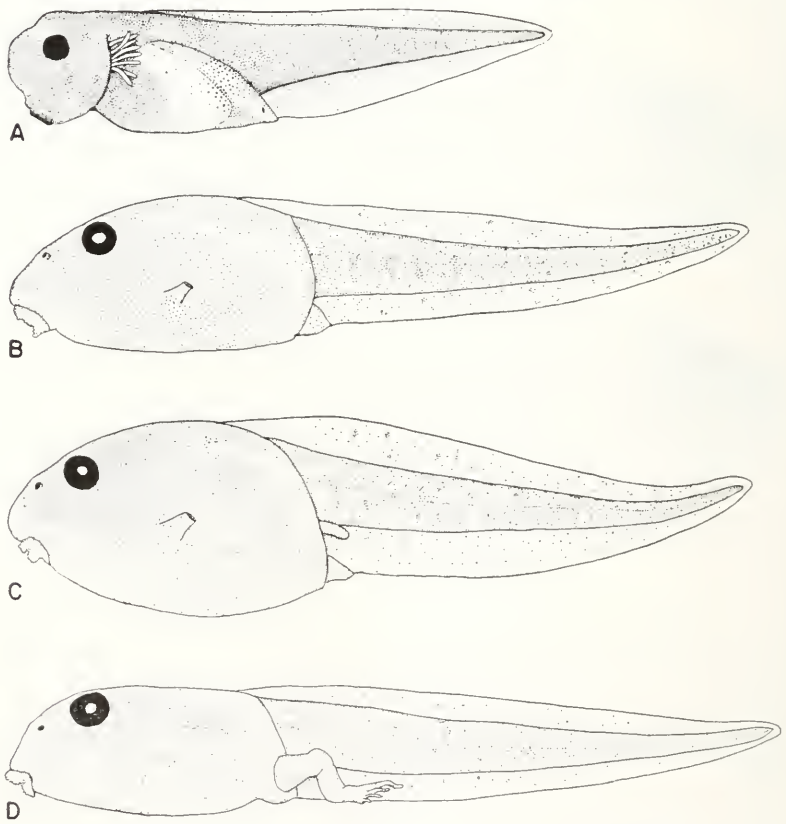


FIG. 13. Tadpoles of *Smilisca phaeota:* (A) Stage 21 (KU 68479) ×14; (B) Stage 25 (KU 68480) ×5; (C) Stage 30 (KU 68482) ×4; (D) Stage 40 (KU 68483) ×3.

pallid than *baudini,* and *cyanosticta* usually is darker than *baudini;* both species have larger dark markings on the tail than does *S. phaeota. Smilisca baudini* has a dark streak on the middle of the anterior one-fourth of the tail (Figs. 11-13).

Smilisca puma is distinctive in having a grayish brown body and dark gray reticulations on the tail. *Smilisca sila* and *sordida* are distinctive in having pairs (sometimes interconnected) of dark marks on the dorsal surfaces of the caudal musculature, and in dorsal view the tail appears to be marked with dark and pale creamy-tan transverse bars. These dark marks, as well as the small flecks on the tail, are brown in *S. sila* and red in *sordida. Smilisca sila* has dark brown flecks on the dorsal surface of the body and small white flecks laterally; these markings are absent in *S. sordida* (Fig. 14).

Descriptions of the coloration of living tadpoles are given in the accounts of the species.

Growth and Development

Information on the growth and development of Middle American hylids is scanty. Adequate descriptions have been published for *Phyllomedusa annae* (Duellman, 1963b), *Phrynohyas venulosa* (Zweifel, 1964), and *Triprion petasatus* (Duellman and Klaas, 1964). Material is available for adequate descriptions of the developmental stages of four species of *Smilisca* (Tables 9-12, Figs. 11-13). Because none of the tadpoles was raised from hatching to metamorphosis, the rate of growth and duration of the larval stages are unknown.

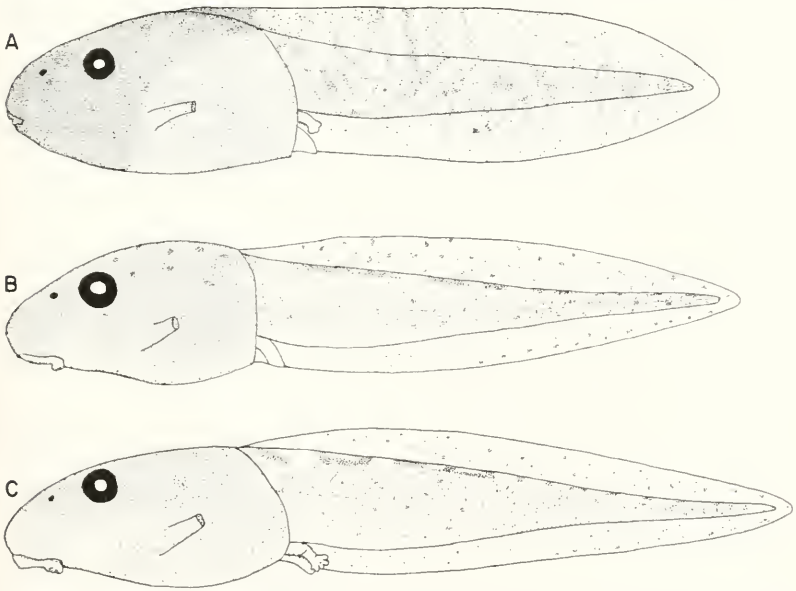


FIG. 14. Tadpoles of *Smilisca*: (A) *S. puma,* Stage 30 (KU 91807); (B) *S. sila,* Stage 25 (KU 80260); *S. sordida,* Stage 30 (KU 68475). All ×3.5.

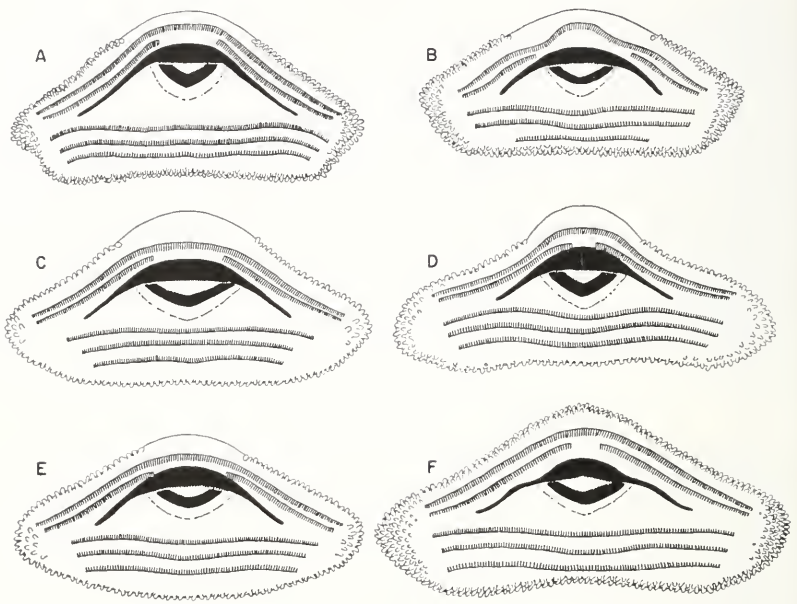


FIG. 15. Mouthparts of tadpoles of *Smilisca;* (A) *S. baudini* (KU 60018); (B) *S. puma* (KU 91807); (C) *S. cyanosticta* (KU 87625); (D) *S. sila* (KU 80620); (E) *S. phaeota* (KU 68482); (F) *S. sordida* (KU 68475). All ×17.

TABLE 9.—GROWTH AND DEVELOPMENT OF TADPOLES OF SMILISCA BAUDINI. (MEANS ARE GIVEN IN PARENTHESES AFTER THE OBSERVED RANGES.)

STAGE	N	Total length	Body length	Tail length
21.....	10	5.1–5.4 (5.22)	2.6–2.7 (2.54)	2.5–2.7 (2.58)
24.....	10	6.0–6.5 (6.20)	2.3–2.6 (2.45)	3.5–3.9 (3.69)
25.....	10	7.2–8.3 (7.78)	3.0–3.3 (3.14)	4.2–5.0 (4.64)
27.....	10	18.5–21.5 (20.22)	8.0–9.0 (8.38)	10.4–13.0 (11.84)
29.....	10	21.5–24.5 (22.60)	8.5–10.0 (9.25)	12.5–14.5 (13.35)
37.....	3	28.5–31.0 (30.00)	11.0–12.5 (11.67)	17.5–19.0 (18.00)
38.....	10	35.0–37.5 (35.50)	12.0–13.5 (12.80)	21.5–24.0 (22.70)
40.....	2	34.0–37.0 (35.50)	12.5–13.5 (13.00)	21.5–23.5 (22.50)
41.....	10	34.0–37.0 (35.50)	12.5–13.5 (13.00)	21.5–23.5 (22.50)
42.....	3	24.0–30.0 (27.00)	12.5–13.0 (12.67)	11.5–17.0 (14.33)
45.....	6	14.0–24.0 (17.58)	12.5–14.0 (13.37)	1.5–10.0 (4.17)
46.....	23	.....	12.0–15.5 (13.34)	.....

TABLE 10.—GROWTH AND DEVELOPMENT OF TADPOLES OF SMILISCA CYANOSTICTA. (MEANS ARE GIVEN IN PARENTHESES AFTER THE OBSERVED RANGES.)

STAGE	N	Total length	Body length	Tail length
21.....	10	5.8–6.5 (6.28)	2.8–3.1 (3.00)	3.0–3.5 (3.28)
25.....	10	7.9–9.2 (8.44)	2.7–3.2 (2.96)	4.8–6.0 (5.48)
30.....	7	22.5–25.0 (23.50)	8.5–9.5 (9.00)	14.0–15.5 (14.57)
36.....	10	27.0–30.0 (28.75)	9.5–11.5 (10.80)	17.0–18.5 (17.95)
42.....	2	26.0–27.0 (26.50)	10.00	16.0–17.0 (16.50)
46.....	2	.....	14.00	.....

Hatchlings of three species (*S. baudini, cyanosticta,* and *phaeota*) are available. These larvae have non-functional eyes and large oral suckers. By the time the larvae have developed to stage 21, external gills are present, the caudal musculature and caudal fin have been differentiated, and the head is distinguishable from the body. In stage 21 oral suckers and a large amount of yolk are still present.

The developmental data on the four species show no significant variations; consequently, we will describe the development of only one species, *Smilisca phaeota* (Table 11, Figs. 13 and 16).

Stage 21.—Bulging cream-colored yolk mass, transparent cornea, and moderately long, unbranched filamentous gills, and oral suckers present; mouth having irregular papillae on lower lip; teeth and beaks absent; caudal myomeres distinct; pigmentation uniform over body and caudal musculature; caudal fin transparent with scattered small flecks.

Stage 25.—Operculum complete; gills absent; sinistral spiracle apparently functional; cloacal tail-piece, nasal capsules, and external nares present; gut

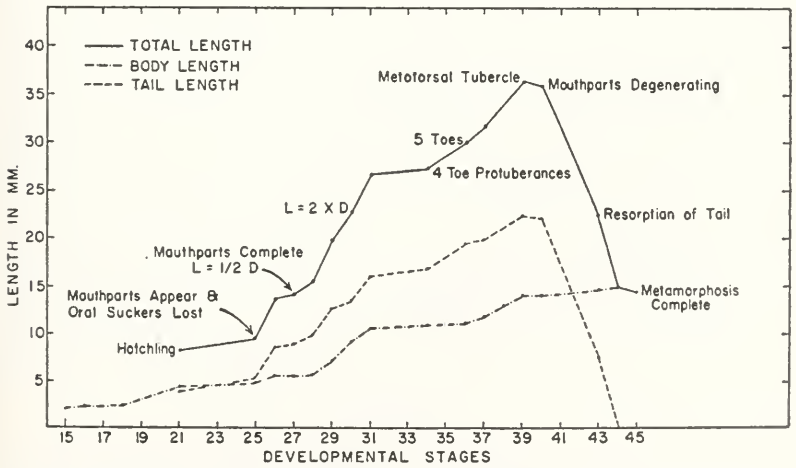


FIG. 16. Relative rate of growth in tadpoles of *Smilisca phaeota* as correlated with developmental stages. Formulas for the limb bud refer to its length (L) in relation to basal diameter (D).

partly formed; mouth bordered by single row of papillae, except medially; small papillae present in lateral fold of lips; two upper and three lower toothrows present, but not fully developed; beaks apparently fully developed; depth of dorsal and ventral fins less than depth of caudal musculature; tip of tail upturned; pigment on body most dense on dorsum and sides; faint, nearly pigmentless crescent-shaped mark on posterior edge of body; concentrations of pigment forming small spots on tail.

Stage 28.—Mouthparts complete; limb bud about half as long as thick; other structural features and coloration closely resemble those in stage 25.

Stage 30.—Limb bud approximately twice as long as thick; body as deep as wide; dorsal fin deepest just posterior to body; ventral fin deeper than caudal musculature; tail sharply upturned distally; anal tube dextral; brown pigment sparse on flanks.

Table 11.—Growth and Development of Tadpoles of Smilisca phaeota. (Means Are Given in Parentheses After the Observed Ranges.)

Stage	N	Total length	Body length	Tail length
15	10	.....	1.9–2.1 (1.97)	.....
16	8	.....	2.0–2.2 (2.07)	.....
18	4	.....	2.2–2.6 (2.31)	.....
21	3	7.9–8.6 (8.21)	4.1–4.5 (4.31)	3.8–4.1 (3.92)
25	10	8.7–10.6 (9.69)	4.5–4.8 (4.64)	4.3–6.0 (5.05)
26	11	12.3–16.1 (14.01)	4.2–6.3 (5.60)	6.7–9.8 (8.41)
27	10	13.0–15.7 (14.28)	4.9–6.2 (5.40)	7.7–10.5 (8.88)
28	13	13.9–20.9 (15.62)	5.2–8.3 (5.75)	8.5–12.6 (9.85)
29	8	17.8–22.3 (19.79)	6.3–8.4 (7.19)	11.5–14.0 (12.60)
30	9	20.3–24.8 (22.85)	8.1–10.5 (9.32)	10.5–15.5 (13.53)
31	5	24.1–28.5 (26.61)	9.4–11.2 (10.59)	14.7–17.3 (16.02)
34	5	24.8–29.4 (27.31)	9.2–11.6 (10.73)	15.6–18.5 (16.80)
36	3	30.0–30.1 (30.07)	10.1–12.2 (11.15)	18.9–20.0 (19.44)
37	4	28.9–34.1 (31.75)	11.5–12.4 (11.88)	17.4–22.5 (19.88)
38	1	28.98	12.88	16.10
39	2	35.6–36.9 (36.25)	14.00	21.6–22.9 (22.25)
40	2	32.3–39.8 (36.05)	14.00	18.3–21.8 (20.05)
43	2	21.5–23.0 (22.25)	14.2–14.8 (14.45)	6.8–8.8 (7.80)
44	4	.....	14.5–15.6 (15.08)	.....
46	11	.....	12.7–16.7 (14.26)	.....

TABLE 12.—GROWTH AND DEVELOPMENT OF TADPOLES OF SMILISCA SORDIDA. (MEANS ARE GIVEN IN PARENTHESES AFTER THE OBSERVED RANGES.)

STAGE	N	Total length	Body length	Tail length
25.....	6	25.5–28.0 (26.1)	9.0–9.5 (9.3)	16.2–18.5 (16.7)
33.....	2	28.5–30.0 (29.3)	10.2–10.5 (10.4)	18.0–19.8 (18.9)
36.....	8	29.5–34.5 (32.3)	10.2–11.7 (10.8)	19.3–23.0 (21.5)
37.....	7	31.6–37.5 (34.6)	11.0–12.5 (11.5)	21.6–25.0 (23.2)
41.....	3	33.0–37.2 (35.2)	11.6–12.2 (11.9)	21.4–25.2 (23.2)
43.....	1	.....	12.4	.....
46.....	9	.....	13.1–15.7 (14.9)	.....

Stages 34, 36, 37, and *38.*—Stage 34, foot paddle-shaped with four toe buds; stage 36, five toe buds; stages 37 and 38, lengthening of toes. In all four stages, spiracle persistent, and pigmentation resembling that of early stages.

Stage 39.—Metatarsal tubercle present; greatest total length (36.9 mm.) attained.

Stage 40.—Subarticular tubercles prominent; skin over forelimbs transparent; cloacal tail-piece and spiracle absent; outer tooth-rows degenerating; caudal fins shallower than in preceding stages; distal part of tail nearly straight; size of dark markings on tail decreased; pigment present on hind limb.

Stage 43.—Forelimbs erupted; larval mouthparts absent; corner of mouth between nostril and eye; transverse bands present on hind limbs; tail greatly reduced (about 8 mm. in length).

Stage 44.—Sacral hump barely noticeable; tail reduced to a stub; corner of mouth at level of pupil of eye; dorsal surfaces pale olive-green; venter white.

Changes proceed in a definite pattern during the growth and development of tadpoles. Larval teeth are absent in hatchlings; the inner tooth-rows develop first, and the third lower row last. At metamorphosis the third lower row is the first to be lost. The tail increases gradually in length relative to the body. In stage 25 the tail is 52.1 per cent of the total length, and in stage 36, 64.6 per cent. In later stages the tail becomes relatively shorter through resorption. Duellman and Klaas (1964:320) noted a great size-variation in *Triprion* tadpoles in stage 25. No such variation is apparent in any stage of any of the species of *Smilisca* studied.

The growth and development of the other species of *Smilisca* do not differ significantly from that of *S. phaeota.* The tadpoles of *S. sila* and *sordida* from streams have relatively longer tails at hatching. For example, in tadpoles of *S. sordida* the average length of tail is 64.0 per cent of the body-length in stage 25, and in stage 37, 67.0 per cent.

Behavior

The tadpoles of *S. baudini, cyanosticta, phaeota,* and *puma* are pelagic inhabitants of shallow ponds. Early stages of *S. baudini* in which external gills

are present have been observed to hang vertically with the gills spread out at the surface of the water, a behavior noted by Zweifel (1964:206) in tadpoles of *Phrynohyas venulosa,* which also develop in warm, standing water having a relatively low oxygen-tension. When disturbed the pelagic tadpoles usually dive and seek shelter amidst vegetation or in mud on the bottom. This behavior was observed in *S. baudini, cyanosticta,* and *phaeota* by day and at night. No tadpoles of *S. puma* were observed by day; those seen at night were near the surface of small water-filled depressions in a grassy marsh; they responded to light by taking refuge in the dense grass. Perhaps tadpoles of this species are negatively phototactic and remain hidden by day.

The stream-inhabiting tadpoles of *S. sila* and *sordida* live in clear pools in rocky streams, where they were observed to cling by their mouths to rocks in the stream and to seek shelter amidst pebbles or beneath rocks and leaves on the bottom. These tadpoles are not found in shallow riffles.

We have not found tadpoles of two species of *Smilisca* in the same body of water and therefore cannot offer observations on ecological relationships in sympatric situations.

PHYLOGENETIC RELATIONSHIPS

Identifiable hylid remains are known from the Miocene to the Recent, but these fossils are mostly fragmentary and provide little useful information regarding the phylogenetic relationships of living genera. Frogs of the genus *Smilisca* are generalized and show no striking adaptations, either in their structure or in their modes of life history.

Interspecific Relationships

In attempting to understand the relationships of the species of *Smilisca* we have emphasized osteological characters. The phylogeny suggested by these characters is supported by other lines of evidence, including external morphology, tadpoles, and breeding calls.

Our concept of the prototype of the genus *Smilisca* is a moderate-sized hylid having: (1) a well-developed frontoparietal fontanelle, (2) frontoparietal lacking lateral processes, (3) no bony squamosal-maxillary arch, (4) a fully ossified ethmoid, (5) paired subgular vocal sac, (6) moderately webbed fingers and toes, (7) relatively few supernumerary tubercles on the digits, (8) eggs deposited in clumps in ponds, (9) anteroventral mouth in tadpoles bordered by one row of labial papillae, but median part of upper lip bare, (10) tail relatively short and deep in tadpoles, and (11) a breeding call consisting of a series of like notes.

Two phyletic lines evolved from this prototype. The first of these was the stock that gave rise to the *baudini* group. The evolutionary changes that took place in this line included increase in size, development of a lateral curvature of the maxillary, and an increased amount of cranial ossification, especially in the dermal roofing bones. This phyletic line retained the larval characters and breeding call of the prototype. The second phyletic line gave rise to the *sordida* group and diverged from the prototype in the development of an angular maxillary and a breeding call consisting of a primary note followed by secondary notes. The frogs in this phyletic line retained the moderate

size of the prototype and did not develop additional dermal bone. Our concept of the phylogenetic relationships is shown graphically in Figure 17.

Within the *baudini* group one stock retained separate nasals and did not develop a bony squamosal-maxillary arch, but broad lateral processes developed on the frontoparietals. The tadpoles remained unchanged from the primitive type. This stock evolved into *S. phaeota.* In the other stock the nasals became fully ossified and a bony squamosal-maxillary arch developed. One branch of this second stock retained tadpoles having only one row of labial papillae and did not develop lateral processes on the frontoparietals; this branch evolved into *S. cyanosticta.* The other branch diverged and gave rise to *S. baudini* by developing relatively shorter hind legs, large lateral processes on the frontoparietals, and tadpoles having two rows of labial papillae.

Within the *sordida* group the cranial features remained unchanged in one line, which gave rise to *S. sila,* whereas in a second line the nasals were reduced, and their long axes shifted with the result that they are not parallel to the maxillaries; the amount of ossification of the ethmoid was reduced, and the tadpoles developed two rows of labial papillae. In this second line one branch retained the pond-breeding habits and gave rise to *S. puma,* whereas a second branch became adapted to stream-breeding and gave rise to *S. sordida.*

Certain aspects of this proposed phylogeny warrant further comment. Features such as the deposition of additional bone that roofs the skull or that forms lateral projections from the frontoparietals, like those in *S. baudini* and *phaeota,* are minor alterations of dermal elements and not basic modifica-

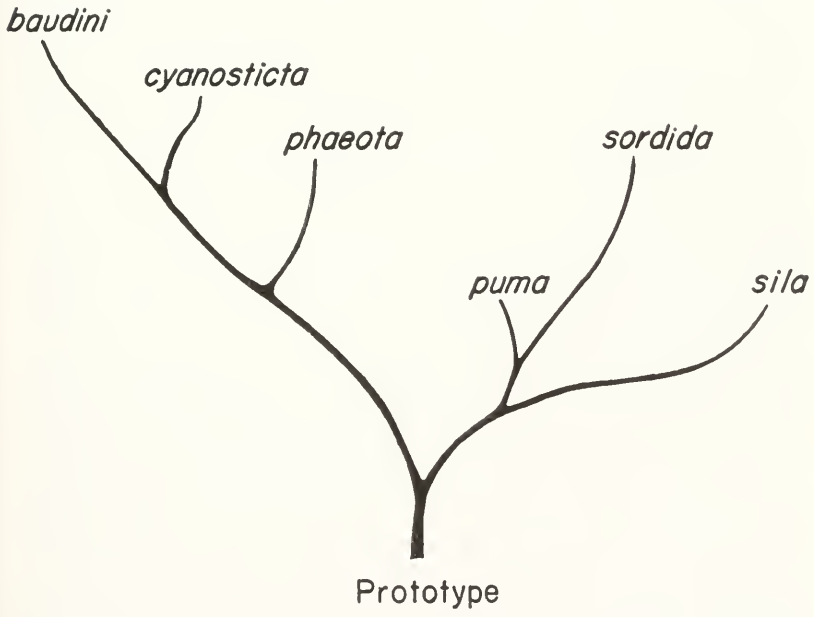


FIG. 17. Hypothesized phylogenetic relationships of the species of *Smilisca.*

tions of the architecture of the skull. Consequently, we hypothesize the independent development of these dermal changes in *S. baudini* and *phaeota*. Similar kinds of dermal modifications have evolved independently in many diverse groups of frogs.

Likewise, we propose the parallel development of stream-adapted tadpoles in *S. sordida* and *sila;* in both cases the tadpoles adapted to changing environmental conditions (see following section on evolutionary history). Tadpoles of *S. sordida* already had two rows of labial papillae before entering the streams; subsequently the tadpoles developed complete rows of papillae, ventral mouths and long tails having low fins. Possibly the tadpoles of *S. sila* had two rows of labial papillae prior to their adapting to stream conditions; in the process of adapting they developed ventral mouths and long tails having low fins. Similar modifications in tadpoles have occurred in many diverse groups of Middle American hylids, such as *Plectrohyla, Ptychohyla,* the *Hyla uranochroa* group, and the *Hyla taeniopus* group.

Our lack of concern about coloration is due to the fact that, with the exception of the blue spots on the flanks and posterior surfaces of the thighs in some species, the coloration of *Smilisca,* consisting of a pattern of irregular dark marks on a paler dorsum and dark transverse bars on the limbs, is not much different from that of many other Neotropical hylids. Blue is a structural color, rare among Amphibia, which is achieved by the absence of lipophores above the guanophores. Thus, the incident light rays at the blue end of the spectrum are reflected by the guanophores without interference by an overlying yellow lipophore screen. According to Noble (1931), lipophores are capable of amoeboid movement that permits shifts in their positions, between or beneath the guanophores. We do not know whether this behavior of lipophores is widespread and is effected in response to environmental changes, or whether it is a genetically controlled attribute that is restricted in appearance. If the latter is the case we must assume that the prototype of *Smilisca* possessed such an attribute which was lost in *S. baudini, phaeota,* and *puma.* The development of blue spots is not constant in *S. sordida* and *S. sila;* in *S. cyanosticta* the spots range in color from blue to pale green.

The coloration of the tadpoles is not distinctive, except for the presence of dorsal blotches on the tails of *S. sila* and *sordida.* However, the similarity in pattern cannot be interpreted as indicating close relationships because nearly identical patterns are present in *Hyla legleri* and some species of *Prostherapis.* This disruptive coloration seems to be directly associated with the pebble-bottom, stream-inhabiting tadpoles.

In the *baudini* group, *S. phaeota* and *cyanosticta* are allopatric, whereas *S. baudini* occurs sympatrically with both of those species. The call of *S. baudini* differs notably from the calls of *S. phaeota* and *cyanosticta,* which are more nearly alike. Although in the phylogenetic scheme proposed here *S. sila* is considered to be more distantly related to *S. puma* than is *S. sordida,* the calls of *S. sila* and *puma* more closely resemble one another than either resembles that of *S. sordida. Smilisca sila* and *puma* are allopatric, whereas *S. sordida* is broadly sympatric with both of those species. We assume that in their respective phyletic lines the differentiation of both *S. baudini* and *sordida* was the result of genetic changes in geographically isolated populations. Subsequently, each species dispersed into areas inhabited by other members of their respective groups. Selection for differences in the breeding calls helped to

reinforce other differences in the populations and thereby aided in maintaining specificity.

Evolutionary History

With respect to temporal and spatial aspects of evolution in *Smilisca*, we have tried to correlate the phylogenetic evidence on *Smilisca* with the geologic data on Middle America presented by Lloyd (1963), Vinson and Brineman (1963), Guzmán and Cserna (1963), Maldonado-Koerdell (1964), and Whitmore and Stewart (1965). Likewise, we have borne in mind the evidence for, and ideas about, the evolution of the Middle American herpetofauna given by Dunn (1931b), Schmidt (1943), Stuart (1950, 1964) Duellman (1958, MS), and Savage (MS).

According to Stuart's (1950) historical arrangement of the herpetofauna, *Smilisca* is a member of the Autochthonous Middle American Faunal Element, and according to Savage's (MS) arrangement the genus belongs to the Middle American Element, a fauna which was derived from a generalized tropical American unit that was isolated in tropical North America by the inundation of the Isthmian Link in early Tertiary, that developed *in situ* in tropical North America, and that was restricted to Middle America by climatic change in the late Cenozoic.

Savage (MS) relied on the paleogeographic maps of Lloyd (1963) to hypothesize the extent and centers of differentiation of the Middle American Faunal Element. According to Lloyd's concept, Middle America in the Miocene consisted of a broad peninsula extending southeastward to about central Nicaragua, separated from the Panamanian Spur of continental South America by shallow seas. A large island, the Talamanca Range, and remnants of the Guanarivas Ridge formed an archipelago in the shallow sea. The recent discovery of remains of mammals having definite North American affinities in the Miocene of the Canal Zone (Whitmore and Stewart, 1965) provides substantial evidence that at least a peninsula was continuous southeastward from Nuclear Central America to the area of the present Canal Zone in early mid-Miocene time. South America was isolated from Central America by the Bolivar Trough until late mid-Pliocene.

Thus, in the mid-Tertiary the broad peninsula of Nuclear Central America, which consisted of low and moderately uplifted regions having a tropical mesic climate, provided the site for the evolution of *Smilisca*. It is not possible to determine when the genus evolved, but to explain the differentiation of the species it is unnecessary to have the ancestral *Smilisca* present prior to the Miocene.

We view the Miocene *Smilisca* as the prototype described in the preceding section, and suppose that it lived in the mesic tropical environment of the eastern part of the Central American Peninsula (in what is now Costa Rica and western Panamá). Two stocks differentiated, probably in middle Miocene times; one of these, the ancestral stock of the *baudini* group, was widespread on the Caribbean lowlands from the Nicaraguan Depression to the Bolivar Trough, and the other, the ancestral stock of the *sordida* group, was restricted to the Pacific lowlands of the same region. In late Miocene time the ancestral stock of the *baudini* group dispersed northwestward around the deep embayment in the Nicaraguan depression into upper Central America (in what is now Honduras and Guatemala) and thence into southern México. Apparently

differentiation took place on each side of the Nicaraguan Depression; the frogs to the south of the depression evolved into *S. phaeota*, whereas those to the north of the depression represented the stock from which *S. baudini* and *cyanosticta* arose. Prior to the uplift of the mountains in the late Miocene and the Pliocene the *baudini-cyanosticta* stock probably was widespread in northwestern Central America. The elevation of the mountains resulted in notable climatic changes, principally the development of sub-humid environments on the Pacific lowlands. The frogs living on the Pacific lowlands became adapted to sub-humid conditions and developed into *S. baudini*. The stock on the Caribbean lowlands remained in mesic environments and evolved into *S. cyanosticta*.

Possibly in the middle Miocene before the Talamanca Range in Costa Rica and western Panamá was greatly uplifted, the ancestral stock of the *sordida* group invaded the Caribbean lowlands of what is now Costa Rica. The subsequent elevation of the Talamanca Range in the Pliocene effectively isolated the ancestral stock of *S. sila* on the Pacific lowlands from the *puma-sordida* stock on the Caribbean lowlands. The former was subjected to the sub-humid conditions which developed on the Pacific lowlands when the Talamanca Range was uplifted. It adapted to the sub-humid environment by living along streams and evolving stream-adapted tadpoles. On the Caribbean side of the Talamanca Range the *puma-sordida* stock inhabited mesic environments. The stock that evolved into *S. puma* remained in the lowlands as a pond-breeding frog, whereas those frogs living on the slopes of the newly elevated mountains became adapted for their montane existence by developing stream-adapted tadpoles and thus differentiated into *S. sordida*.

Probably the six species of *Smilisca* were in existence by the end of the Pliocene; at that time a continuous land connection existed from Central America to South America. The climatic fluctuations in the Pleistocene, and the post-Wisconsin development of present climatic and vegetational patterns in Middle America, brought about the present patterns of distribution of the species. From its place of origin on the Caribbean lowlands of lower Central America, *S. phaeota* dispersed northward into Nicaragua and southward along the Pacific slopes of northwestern South America. Perhaps in the late Pleistocene or in post-Wisconsin time when mesic conditions were more widespread than now, *S. phaeota* moved onto the Pacific lowlands of Costa Rica. Its route could have been through the Arenal Depression. Subsequent aridity restricted its range on the Pacific lowlands to the Golfo Dulce region. Climatic fluctuation in northern Central America restricted the distribution of *S. cyanosticta* to mesic habitats on the slopes of the Mexican and Guatemalan highlands and to certain humid areas on the lowlands. *Smilisca baudini* was well adapted to sub-humid conditions, and the species dispersed northward to the Rio Grande Embayment and to the edge of the Sonoran Desert and southward into Costa Rica. In southern México and Central America the species invaded mesic habitats. Consequently, in some areas it is sympatric with *S. cyanosticta* and *phaeota*.

Smilisca puma dispersed northward onto the Caribbean lowlands of southern Nicaragua. Its southward movements probably were limited by the ridges of the Talamanca Range that extend to the Caribbean coast in the area of Punta Cahuita in Costa Rica. *Smilisca sila* dispersed along the Pacific lowlands and slopes of the mountains from eastern Costa Rica and western Panamá through

eastern Panamá to northern Colombia. Climatic fluctuation in the Pleistocene evidently provided sufficient altitudinal shifts in environments in the Talamanca Range to permit S. *sordida* to move onto the Pacific slopes. From its upland distribution the species followed streams down to both the Caribbean and Pacific lowlands, where it is sympatric with S. *puma* on the Caribbean lowlands and S. *sila* on the Pacific lowlands.

The evolution of the species-groups of *Smilisca* was effected through isolation by physical barriers in the Cenozoic; the differentiation of the species was initiated by further isolation of populations by changes in physiography and climate. Present patterns of distribution resulted from Pleistocene and post-Wisconsin climatic changes. Today, sympatric species have different breeding habits and breeding calls which reinforce the differences in morphology.

SUMMARY AND CONCLUSIONS

The genus *Smilisca* is composed of six species of tree frogs; each species is defined on the basis of adult morphology, larval characters, and breeding behavior. Keys are provided to aid in the identification of adults and of tadpoles.

Analysis of the characters and examination of type specimens indicates that several currently-recognized taxa are synonymous, as follows:

1. *Hyla beltrani* Taylor, 1942 = *Smilisca baudini.*
2. *Hyla gabbi* Cope, 1876 = *Smilisca sordida.*
3. *Hyla manisorum* Taylor, 1954 = *Smilisca baudini.*
4. *Hyla nigripes* Cope, 1876 = *Smilisca sordida.*
5. *Hyla wellmanorum* Taylor, 1952 = *Smilisca puma.*

Smilisca phaeota cyanosticta Smith, 1953 is elevated to specific rank, and one new species, *Smilisca sila,* is named and described.

The skeletal system of developmental stages and the adult of *Smilisca baudini* is described, and the skull is compared with that of other members of the genus.

The tadpoles are described, compared, and illustrated; the larval development of *Smilisca phaeota* is described.

Breeding behavior and breeding calls are described and compared. Some species of *Smilisca* have breeding choruses. Two species, S. *sila* and *sordida,* breed in streams, whereas the others breed in ponds.

The genus is considered to be part of the Middle American Faunal Element: the species are thought to have differentiated in response to ecological diversity and historical opportunities provided by Cenozoic changes in physiography and climate.

LITERATURE CITED

Baird, S. F.
1854. Descriptions of new genera and species of North American frogs. Proc. Acad. Nat. Sci. Philadelphia, 7:59-62. April 27.
1859. Reptiles of the boundary. United States and Mexican boundary survey. Washington, D. C., p. 35, pl. 41.

Baldauf, R. J.
1959. Morphological criteria and their use in showing bufonid phylogeny. Jour. Morph., 104:527-560. May.

Barbour, T.
1923. Notes on reptiles and amphibians from Panama. Occas. Papers Mus. Zool. Univ. Michigan, 129:1-16. January 25.

Blair, W. F.
1959. Call structure and species groups in U. S. treefrogs (*Hyla*). Southwest. Nat., 3:77-89. June 1, 1959.
1962. Non-morphological data in anuran classification. Syst. Zool., 11:72-84. June.
1963. Evolutionary relationships of North American toads of the genus Bufo: A progress report. Evolution, 17:1-16. March.

Bogert, C. M.
1960. The influence of sound on the behavior of amphibians and reptiles. *in* Lanyon, W. E. and Tavolga, W. N. (Eds.) Animal sounds and communication, pp. 137-320.

Brattstrom, B. H.
1957. The phylogeny of the Salientia based on skeletal morphology. Syst. Zool., 6:70-74. June.

Breder, C. M., Jr.
1946. Amphibians and reptiles of the Rio Chucunaque drainage, Darien, Panama, with notes on their life histories and habits. Bull. Amer. Mus. Nat. Hist., 86:375-436, pls. 42-60. August 26.

Brocchi, P.
1877. Note sur quelques batrachiens hylaeformes recuilles au Mexique et au Guatemala. Bull. Soc. Philom. Paris, ser. 7, 1:122-132.

Carvalho, A. L.
1954. A preliminary synopsis of the genera of American microhylid frogs. Occas. Papers Mus. Zool. Univ. Michigan, 555:1-19, pl. 1. July 16.

Cochran, D. M.
1961. Type specimens of reptiles and amphibians in the United States National Museum. Bull. U. S. Nat. Mus., 220:xv + 291 pp.

Cope, E. D.
1862. Catalogues of the reptiles obtained during the explorations of the Parana, Paraguay, Vermejo and Uraguay rivers . . . Proc. Acad. Nat. Sci. Philadelphia, 14, pt. 9:346-359.
1865. Third contribution to the herpetology of tropical America. Proc. Acad. Nat. Sci. Philadelphia, 17:185-198. October.
1871. Ninth contribution to the herpetology of tropical America. Proc. Acad. Nat. Sci. Philadelphia, 23, pt. 2:200-224.

Copland, S. J.
1957. Australian tree frogs of the genus *Hyla*. Proc. Linnean Soc. New South Wales, 82, pt. 1:9-108. September.

Duellman, W. E.
1956. The frogs of the hylid genus *Phrynohyas* Fitzinger, 1843. Misc. Publ. Mus. Zool. Univ. Michigan, 96:1-47, pls. 1-6. February 21.
1958. A monographic study of the colubrid snake genus *Leptodeira*. Bull. Amer. Mus. Nat. Hist., 114:1-152, pls. 1-31. February 24.

1963a. A review of the Middle American tree frogs of the genus Ptychohyla. Univ. Kansas Publ. Mus. Nat. Hist., 15:297-349, pls. 11-18. October 18.

1963b. A new species of tree frog, genus *Phyllomedusa*, from Costa Rica. Rev. Biol. Trop., 11(1):1-23. October.

1964. A review of the frogs of the Hyla bistincta group. Univ. Kansas Publ. Mus. Nat. Hist., 15:469-491. March 2.

1965. Frogs of the *Hyla taeniopus* group. Copeia, no. 2:159-168. June 25.

DUELLMAN, W. E. and KLAAS, L. T.
1964. The biology of the hylid frog *Triprion petasatus*. Copeia, no. 2: 308-321. June 30.

DUMÉRIL, A. M. C. and BIBRON, G.
1841. Erpétologie Générale ou histoire naturelle complète des reptiles, vol. 8, 792 pp.

DUNN, E. R.
1931a. The amphibians of Barro Colorado Island. Occas. Papers Boston Soc. Nat. Hist., 5:403-421. October 10.

1931b. The herpetological fauna of the Americas. Copeia, no. 3:106-119. October 30.

1944. Herpetology of the Bogotá area. Rev. Acad. Colombiana Cien. Exact., Fis. Nat., 6:68-81.

FOUQUETTE, M. J., JR.
1960. Isolating mechanisms in three sympatric tree frogs in the Canal Zone. Evolution, 14:484-497. December.

FUNKHOUSER, ANNE
1957. A review of the neotropical tree-frogs of the genus *Phyllomedusa*. Occas. Papers Nat. Hist. Mus. Stanford Univ., 5:1-89. April 1.

GADOW, H.
1908. Through southern Mexico. London, Witherby and Co. xvi + 527 pp.

GAIGE, H. T., HARTWEG, N. and STUART, L. C.
1937. Notes on a collection of amphibians and reptiles from eastern Nicaragua. Occas. Papers Mus. Zool. Univ. Michigan, 357:1-18. October 26.

GOIN, C. J.
1961. Synopsis of the genera of hylid frogs. Ann. Carnegie Mus., 36:5-18. July 14.

GOSNER, K. L.
1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica, 16:183-190. September 23.

GRIFFITHS, I.
1959. The phylogeny of *Sminthillus limbatus* and the status of the Brachycephalidae (Amphibia, Salientia). Proc. Zool. Soc. London, 132:457-487, pls. 1-4.

GUZMÁN, E. J. and CSERNA, Z.
1963. Tectonic History of Mexico. Amer. Assoc. Petrol. Geol., Mem. 2:113-129.

HECHT, M. K.
1962. A reevaluation of the early history of the frogs. Part I. Syst. Zool., 11:39-44. March.

1963. A reevaluation of the early history of the frogs. Part II. Syst. Zool., 12:20-35. March.

JOHNSON, C.
1959. Genetic incompatibility in the call races of *Hyla versicolor* Le Conte in Texas. Copeia, no. 4:327-335. December 30.

Lloyd, J. J.
1963. Tectonic history of the south Central-American Orogen. Amer. Assoc. Petrol. Geol., Mem. 2:88-100.

Maldonado - Koerdell, M.
1964. Geohistory and paleogeography of Middle America, *in* Wauchope, R. and West, R. C. (Eds.). Handbook of Middle American Indians, vol. 1, Univ. Texas Press, Austin, 570 pp.

Maslin, T. P.
1963. Notes on some anuran tadpoles from Yucatán, México. Herpetologica, 19:122-128. July 3.

Mittleman, M. B. and List, J. C.
1963. The generic differentiation of the swamp treefrogs. Copeia, no. 2:80-83. May 29.

Noble, G. K.
1931. The biology of the amphibia. McGraw Hill, New York, 577 pp.

Orton, G. L.
1957. The bearing of larval evolution on some problems in frog classification. Syst. Zool., 6:79-86. June.

Peters, W.
1863. Mittheilungen uber neue Batrachier. Monats. Konigl. Akad. Wiss. Berlin, pp. 445-471.
1873. Uber eine neue Schildkrötenart, *Cinosternon Effeldtii* und einige andere neue oder weniger bekannte Amphibien. Monats. Konigl. Akad. Wiss. Berlin, pp. 603-618, pl. 5. October 16.

Rivero, J. A.
1961. Salientia of Venezuela. Bull. Comp. Zool., 126:1-207. November.

Savage, J. M. and Carvalho, A. L.
1953. The family position of Neotropical frogs currently referred to the genus *Pseudis*. Zoologica, 38:193-200.

Schmidt, K. P.
1941. The amphibians and reptiles of British Honduras. Zool. Ser. Field Mus. Nat. Hist., 22:475-510. December 30.
1943. Corollary and commentary for "Climate and Evolution." Amer. Midl. Nat., 30:241-253. July.

Schmidt, O.
1857. Diagnosen neuer Frösche des zoologischen Cabinets zu Krakau. Sitzungb. Konigl. Akad. Wiss. Math.-Natur. Cl., 24(1):10-15. March.
1858. Deliciae Herpetogicae Musei Zoologici Cracoviensis. Denkschr. K. K. Akad. Wiss. Math.-Natur. Cl., 14(2):237-258, pls. 1-3.

Smith, H. M.
1953. A new subspecies of the treefrog *Hyla phaeota* Cope of Central America. Herpetologica, 8:150-152. January 30.

Smith, H. M. and Taylor, E. H.
1950. Type localities of Mexican reptiles and amphibians. Univ. Kansas Sci. Bull., 33:313-380. March 20.

Starrett, P.
1960. A redefinition of the genus *Smilisca*. Copeia, no. 4:300-304. December 30.

Stebbins, R. C. and Hendrickson, J. R.
1959. Field studies of amphibians in Colombia, South America. Univ. California Publ. Zool., 56:497-540. February 17.

Stokely, P. S. and List, J. C.
1954. The progress of ossification in the skull of the cricketfrog *Pseudacris nigrita triseriata*. Copeia, no. 3:211-217. July 29.

STUART, L. C.
1935. A contribution to a knowledge of the herpetology of a portion of the savanna region of central Petén, Guatemala. Misc. Publ. Mus. Zool. Univ. Michigan, 29:1-56, pls. 1-4, 1 map. October 1.
1948. The amphibians and reptiles of Alta Verapaz, Guatemala. Misc. Publ. Mus. Zool. Univ. Michigan, 69:1-109. June 12.
1950. A geographic study of the herpetofauna of Alta Verapaz, Guatemala. Contr. Lab. Vert. Biol., 45:1-77, pls. 1-9, 1 map. May.
1954. Herpetofauna of the southeastern highlands of Guatemala. Contr. Lab. Vert. Biol., 68:1-65, pls. 1-4. November.
1958. A study of the herpetofauna of the Uaxactun-Tikal area of northern El Peten, Guatemala. Contr. Lab. Vert. Biol., 75:1-30. June.
1961. Some observations on the natural history of tadpoles of *Rhinophrynus dorsalis* Dumeril and Bibron. Herpetologica, 17:73-79. July 11.
1964. Fauna of Middle America, *in* Wauchope, R. and West, R. C. (Eds.). Handbook of Middle American Indians, vol. 1, Univ. Texas Press, Austin, 570 pp.

TAYLOR, E. H.
1942. New Caudata and Salientia from México. Univ. Kansas Sci. Bull., 28:295-323. November 15.
1952. The frogs and toads of Costa Rica. Univ. Kansas Sci. Bull., 35: 577-942. July 1.
1954. Additions to the known herpetological fauna of Costa Rica with comments on other species. No. I. Univ. Kansas Sci. Bull., 36:597-639. June 1.

TAYLOR, E. H. and SMITH, H. M.
1945. Summary of the collections of amphibians made in México under the Walter Rathbone Bacon Traveling Scholarship. Proc. U. S. Natl. Mus., 95:521-613, pls. 18-32. June 30.

TIHEN, J. A.
1962. Osteological observations on New World Bufo. Amer. Midl. Nat., 67:157-183. January.
1965. Evolutionary trends in frogs. Amer. Zoologist, 5:309-318.

VINSON, G. L. and BRINEMAN, J. H.
1963. Nuclear Central America, hub of Antillean Transverse Belt. Amer. Assoc. Petrol. Geol., Mem. 2:101-112.

WHITMORE, F. C., JR. and STEWART, R. H.
1965. Miocene mammals and Central American seaways. Science, 148: 180-185. April 9.

ZWEIFEL, R. G.
1956. Two pelobatid frogs from the Tertiary of North America and their relationships to fossil and Recent forms. Amer. Mus. Novitates, 1762:1-45. April 6.
1958. Results of the Archbold Expeditions. No. 78. Frogs of the Papuan hylid genus *Nyctimystes*. Amer. Mus. Novitates, 1896:1-51. July 22.
1964. Life history of *Phrynohyas venulosa* (Salientia: Hylidae) in Panamá. Copeia, no. 1:201-208. March 26.

Transmitted March 14, 1966.

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Birds From North Borneo

BY

MAX C. THOMPSON

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BY

MAX C. THOMPSON

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Birds From North Borneo

BY

MAX C. THOMPSON

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INTRODUCTION

The major part of this report is an account of birds collected by the expedition of the Bernice P. Bishop Museum of Honolulu, Hawaii, to North Borneo, from June 24, 1962, through January 14, 1963. Most of the time spent in the then British Colony was devoted to collecting in lowland habitats. The chief collecting localities were in the vicinity of Quoin Hill on the Semporna Peninsula, and near Kalabakan. Approximately two weeks were spent in surveying the Tenom area. Additional work was done by the North Borneo Department of Agriculture after my departure, mainly by Antonio D. Garcia.

ACKNOWLEDGMENTS

I am indebted to J. L. Gressitt of the Entomology Department of the Bishop Museum for providing the opportunity for me to work on the expedition and to examine and report on the material collected. Without the help of the North Borneo Department of Agriculture, the success of our expedition would have been restricted. The Entomologist of North Borneo, G. R. Conway, was of great help with our logistic problems as was the Director of the Department, Mr. E. J. H. Berwick, and the Agronomist of Cocoa Research Station, Ed Wyrley-Birch. The Bombay Burmah Trading Corporation, Ltd., provided facilities and transportation at Kalabakan. Mr. Dai Rees of that corporation should be especially mentioned. Others who helped are: J. A. Comber, Ronnie Young, Mr. and Mrs. Horace Traulsen, Maureen Wyrley-

Birch, and the Resident, Tawau, Mr. Peter Edge. The Conservator of Forests kindly provided the necessary permits for collecting.

Authorities of the United States National Museum and The American Museum of Natural History generously permitted me to work at those institutions, using their specimens for comparative studies. Other specimens were borrowed from the Museum of Comparative Zoology, Rijksmuseum Van Natuuriijke Historie, British Museum (Natural History), and the Yale Peabody Museum. Dr. Alexander Wetmore, Herbert Deignan, and Charles Vaurie helped with some of the more difficult taxonomic problems. Specimens cited in this report are in the Bernice P. Bishop Museum, The University of Kansas Museum of Natural History, The University of Michigan Museum of Zoology, and the U. S. National Museum.

Richard F. Johnston and Robert M. Mengel kindly read the manuscript and made many helpful suggestions. The latter re-read it and assisted with the editing.

The most recent comprehensive work published previous to my preparation of manuscript for the present account was Smythies (1960) "The Birds of Borneo."

This report is a partial result of field work supported by a grant from the United States Army Medical Research and Development Command, Department of the Army, to the Bernice P. Bishop Museum for research on ectoparasites of vertebrates. The contract numbers were DA-MD-49-193-62-G47 and G65. The Chapman Fund of The American Museum of Natural History met part of the cost of transporting, to and from the United States, specimens from North Borneo collected after I left there.

METHODS

While collecting at Quoin Hill, we used only guns in taking birds. At an area 12 miles north of Kalabakan, we supplemented the guns with mist nets in the primary forest. This method was excellent for taking rarely seen species. For example the thrush *Zoothera interpres* was never seen in the field but was taken several times in mist nets.

Another method of collecting was the use of native snares. Such snares were made of heavy nylon string tied to a sapling, held down by a nylon string attached to a treadle. When a bird stepped on the treadle, it tripped the snare and a loop closed about its feet, hoisting it aloft. To divert large ground birds and mammals into the snare, natives placed brush barriers along the top of a ridge for one or two miles. Animals were diverted by these barriers until they came to an opening; if they went through they usually tripped the trap. Pheasants and the large ground cuckoo were taken in this manner.

NOTES ON ZOOGEOGRAPHY

The avifauna of Borneo is of Indo-Malayan affinities. The number of birds endemic to Borneo is relatively small; most species are shared with the Asian mainland. Only 29 birds are known to be endemic to the island and 17 of these are montane. The large proportion of montane endemics is not surprising, because Borneo

has been connected with the Asian continent in recent geological time; lowland isolation, and differentiation, has been less extensive than the montane. The Sunda Shelf, on which Borneo is situated, lies in a shallow sea generally less than 300 feet deep. Beaufort has shown that the Malay Peninsula, Sumatra, and Java were connected until early historic times (Darlington, 1957:488).

The endemic species in Borneo are members of four, possibly five, genera that are also endemic. Four of these five genera are montane in distribution. The only endemic for which the geographic history cannot be adequately explained is the monotypic *Pityriasis gymnocephala*. Its affinities seem to be with the Cracticidae of New Guinea and Australia. The species has been found throughout Borneo. Since *Pityriasis* is endemic to Borneo, it probably was detached from the parent stock at an early period. The Australasian affinities of *Pityriasis* emphasize its zoogeographical peculiarities. A more detailed discussion of this species appears in the annotated list below.

COLLECTING LOCALITIES AND COLLECTORS

1. Cocoa Research Station, Quoin Hill, elevation 750 feet, Tawau. Max C. Thompson (MCT) and Antonio D. Garcia (ADG).

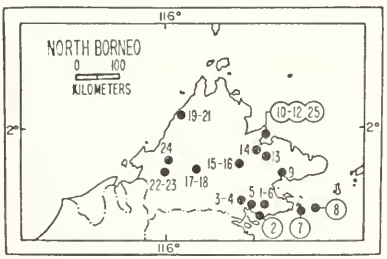

FIG. 1. Localities from which collectors from the Department of Agriculture or I saved specimens in North Borneo.

2. Tawau. Max C. Thompson.

3. Twelve miles north of Kalabakan, elevation 600 feet. Max C. Thompson.

4. Kalabakan, elevation 50 feet. Max C. Thompson.

5. Tiger Estate, 20 miles northwest of Tawau. Max C. Thompson, Antonio D. Garcia.

6. Ulu Balung Cocoa Estate, Mile 27, Quoin Hill, elevation 750 feet, Tawau. Antonio D. Garcia.

7. Karindingen Island. Max C. Thompson.

8. Siamil Island. Max C. Thompson.

9. Lahad Datu. Antonio D. Garcia.

10. Kuala Sumawang, 25 miles west of Sandakan. Antonio D. Garcia.

11. Agricultural Station, Mile 17, Sandakan (Gum-Gum). Antonio D. Garcia.

12. One-fourth mile east Gum-Gum, Sandakan. Antonio D. Garcia.

13. Lamag, Kinabatangan River. Antonio D. Garcia.

14. Pintasan Agriculture Station, Kinabatangan River. Antonio D. Garcia.

15. Kampong Kuamut, Kinabatangan River. Antonio D. Garcia.

16. Kampong Maluwa, Kinabatangan River. Antonio D. Garcia.

17. Ka-Karis, Kinabatangan River, elevation 200 feet. Antonio D. Garcia.

18. Tongod, Kinabatangan River, elevation 300 feet. Antonio D. Garcia.

19. Tuaran. Max C. Thompson, Antonio D. Garcia, S. F. W. Chong (SFWC).

20. Telipok. Antonio D. Garcia, G. R. Conway.

21. Mt. Rumas, 5 miles northwest of Tuaran, elevation 75 feet, Antonio D. Garcia.

22. Five and one-half miles southwest of Tenom, elevation 4,000 feet. Max C. Thompson.

23. Tenom, elevation 600 feet. Max C. Thompson.

24. Kampong Banjar, Mile 29, Keningau. Antonio D. Garcia.

25. Oil Palm Research Station, Mile 32, elevation 40 feet, Sandakan. Antonio D. Garcia.

ECOLOGY OF THE COLLECTING LOCALITIES

Quoin Hill.—At this locality I recognized five habitat types as follows:

Primary forest.—We were fortunate to be able to work at Quoin Hill because it had been opened to cultivation (of Cocoa, *Theobroma cacao*) for only a few years. Thus the primary forest here started at the edge of the Cocoa Research Station. This was in marked contrast to areas on the west coast, where one would need to travel many miles inland to find virgin forest. The forest at Quoin Hill was typical tropical rain-forest, composed mostly of dipterocarps (Dipterocarpaceae). These comprise an essentially Indo-Malayan family, members of which are so conspicuous that we commonly referred to it as Evergreen Dipterocarp Forest. The lowland forests of Borneo are composed of approximately 3,000 species of trees (Browne, 1955). At Quoin Hill, as in most of the tropical rain-forest of Borneo, the forest canopy is stratified in three layers, a distinct and easily recognizable top story and less easily separable middle and lower stories. The top canopy is composed of foliage of giant trees that may tower to heights of 200 feet and have trunks three to seven feet in diameter. The trunk is usually unbranched for 50 to 100 feet and the whole tree is supported by buttresses jutting out from the main trunk. Some of the most important plants in the tropical rain-forest are the strangler figs (*Ficus* sp.). These plants, when in fruit, draw birds in large flocks to feed upon them. Such figs were common about the edges of the research station and some birds taken from these trees were never taken elsewhere. The birds seemed to wait for a certain degree of ripeness of fruits; on one day the figs were unmolested and the next day the trees would be swarming with birds. Strangler fig trees reach tremendous size and help form the upper forest canopy.

The middle and lower forest canopies are not easily separable and I shall speak of them together. The trees forming these varied from 10 to 60 feet in height. The ground surface beneath the trees was usually bare except for leaf litter and dead branches. Sunlight penetrates only where the big trees have been removed or where the larger trees are otherwise widely spaced. At Quoin Hill the large trees of species affording lumber of commercial quality had been taken out, modifying somewhat the character of the forest. Such forest actually contained many of the animals characteristic of primary forest, and I refer to it as badly disturbed primary forest.

Secondary forest.—In some of the areas adjoining the research station, roads had been bulldozed for future expansion and trees had been cut. These areas were starting to grow dense stands of grass and shrubs and will be jungle in a few years unless cut back. Most of the trees in this area are saplings with some trees as large as a foot in diameter.

Fluviatile waters.—There are numerous small streams in the Quoin Hill area, the largest being the Balung River and Apas River. Little work was done along these streams and only the thrushes of the genus *Enicurus* and some kingfishers seemed to be confined to them.

Cocoa plantations.—Artificial plantings of cocoa, *Theobroma cacao*, formed a major habitat type at Quoin Hill, and provided a major source of food for birds. Cocoa planters have found it necessary to provide shade with trees of some other species. In some instances trees from the original primary forest were left standing to provide this shade, but more often exotic trees were planted. Most of the shade trees were of no use to birds save for providing resting places. *Trema orientalis* was the most important in providing food for birds. Its fruit was used more by the frugivorous species of birds than that of any other tree in the cocoa plantings. Tree Cassava, an exotic, was constantly attended by the nectariniids, or honey creepers.

Although the cocoa plantings did not provide much plant material for bird food, they did apparently nourish a horde of insects, which the birds fed upon. A Drongo-cuckoo, *Surniculus lugubris*, had 50 caterpillars in its stomach. Healthy cocoa trees were sparsely inhabited by birds but areas that were obviously infested with insects literally swarmed with birds. Dead shade trees in the cocoa plantings also provided food for woodpeckers, with four species being found utilizing these dead trees.

Abaca.—The last of the habitat types that I recognized at Quoin Hill was a small grove of Abaca, *Musa textilis*, and wild bananas, *Musa* sp. This habitat type was frequented by spiderhunters (*Arachnothera* sp.) of the family Nectariniidae.

KALABAKAN.—We worked at three localities in this area: 12 miles north of Kalabakan, Brantian Estate, and Kalabakan.

Primary forest.—We were fortunate in being able to work on the very edge of the primary forest 12 miles north of Kalabakan. The composition of the primary forest was much like that at Quoin Hill and will not be discussed further. About a month after we arrived at our forest camp, logging crews moved in and cut the commercial timber near our area. The only immediately noticeable difference in the makeup of the avifauna after destruction of the forest canopy was the appearance of the drongo *Dicrurus aeneus*. This drongo was seen in areas where the trees had been cut, sitting on limbs and darting out after insects.

Secondary forest.—The area around Kalabakan proper was in secondary forest, which was almost impossible to penetrate. At Kalabakan, *Cymbirhynchus macrorhynchus*, *Cecropsia striolata*, and *Macronous ptilosus* were taken and I did not see them elsewhere. Kalabakan is situated on the Kalabakan River at the upper tidal limit. The Nipa-Mangrove association, not investigated, lies immediately below Kalabakan.

The Brantian Estate area was mostly in secondary forest and was situated on the Brantian River. There were some fairly large areas of grass with water buffalo wallows in them. These grassy areas were favorite haunts of the Painted Quail, *Coturnix chinensis*.

TENOM.—The first locality that we investigated was 5.5 miles southwest of Tenom, approximately 4,000 feet elevation, in moss forest. A few days were spent collecting in the area of Tenom itself.

Moss forest.—The lower altitudinal limit of the moss forest was about 3,600 feet. The trees on top of the mountain were mostly oaks (*Quercus*) and were festooned with ferns, orchids, and other epiphytes. The area had been used as a triangulation station by a survey team and a small area on top of the mountain had been cleared earlier. At the time of our visit this small area had grown to secondary vegetation, mostly *Pandanus*. The oaks in the primary forest surrounding this disturbed area were generally about 30 to 50 feet high and there was little undergrowth in virgin stands. This area was usually swathed in fog from three o'clock in the

afternoon until eleven o'clock the next morning. One morning of our fourteen there was clear.

Paddy.—The area visited at Tenom itself consisted mostly of old paddy grown to grass and scrub. Forest did occur but was of secondary nature in the immediate vicinity of Tenom.

Siamil Island.—This island is about one mile in circumference and the highest point is about 300 feet above sea level. The island has high bluffs on three sides but slopes gently to the sea on the other. There were patches of forest left on the island, one on the north side and one on the south. The sheer bluffs on the east side of the island were covered with *Pandanus* sp. The undergrowth of the north forest had been cut, leaving extensive bare areas. The principal undergrowth was rattan. The natives are clearing and planting more of the island to coconuts and hope eventually to clear it completely.

Karindingen Island.—This island, about half a mile in circumference and between 10 and 20 feet above sea level at its highest point, was surrounded by extensive coral reefs and sand; the principal vegetation was mangroves.

ECOLOGICAL AFFINITIES OF THE AVIFAUNA AT QUOIN HILL

More time was spent at Quoin Hill than at any other locality. Fifty five of the more common and hence best-known birds are listed in Table 1 together with their primary and secondary preferences of habitat. The habitat distribution of the birds shows the amount of secondary utilization of habitats by birds that occurred predominantly in one habitat. Cocoa was utilized by 6.2 per cent of the birds of the primary forest, and 88.8 per cent of birds of the secondary forest. This indicates that cocoa is an effective substitute for secondary forest for some birds. Of the species of the primary forest, 18.7 per cent occurred also in secondary forest; thus, three times as many species of primary forest utilized secondary forest as utilized cocoa. This too might be expected, since "secondary" forest is of frequent natural occurrence and an ancient feature while the comparatively simple cocoa plantings are new and artificial.

The avifauna at Quoin Hill was a mixture of montane, submontane, and lowland species. Smythies (1957:527) defines four altitudinal areas of distribution: Higher Montane, Montane, Submontane, and Lowland. Higher Montane birds have not been

TABLE 1.—Habitat preferences of 55 Quoin Hill birds.

X=Primary O=Secondary SPECIES	Primary forest	Secondary forest	Cocoa plantations	Fluviatile water	Abaca
Treron curvirostra	...	X	...	...	...
Cacomantis merulinus	...	O	X	...	...
Chalcites malayanus	...	...	X	...	...
Phaenicophaeus chlorophaeus	...	O	X	...	...
Harpactes diardi	X	...	...	...	...
Harpactes duvauceli	X	...	...	...	...
Alcedo euryzona	...	...	...	X	...
Ceyx erithacus	X	...	...	...	...
Eurystomus orientalis	...	X	O	...	...
Calorhamphus fuliginosus	...	O	X	...	...
Megalaima chrysopogon	...	X	O	...	...
Megalaima henrici	X	...	O	...	...
Sasia abnormis	O	X	...	...	...
Meiglyptes tukki	...	X	...	...	...
Dryocopus javensis	...	X	O	...	...
Chrysocolaptes validus	...	O	X	...	...
Eurylaimus ochromalus	...	O	X	...	...
Pitta guajana	X	...	...	...	...
Coracina fimbriata	...	...	X	...	...
Aegithina viridissima	...	...	X	...	...
Chloropsis cyanopogon	...	X	...	...	...
Irena puella	...	X	...	...	...
Pycnonotus brunneus	...	...	X	...	...
Criniger bres	...	X	O	...	...
Criniger phaeocephalus	X	...	...	...	...
Criniger finschii	...	...	X	...	...
Hypsipetes criniger	...	X	O	...	...
Copsychus pyrrhopygus	X	...	...	...	...
Copsychus stricklandi	...	X	O	...	...

X=Primary O=Secondary SPECIES	Primary forest	Secondary forest	Cocoa plantations	Fluviatile water	Abaca
Enicurus ruficapillus	...	...	...	X	...
Pellorneum capistratus	X	...	...	...	...
Trichastoma malaccense	X	O	...	...	...
Trichastoma sepiarium	...	X	...	...	...
Malacopteron magnum	X	O	...	...	...
Malacopteron magnirostre	X	O	...	...	...
Kenopia striata	X	...	...	...	...
Stachyris poliocephala	...	X	...	...	...
Alcippe brunneicauda	X	...	O	...	...
Orthotomus atrogularis	...	X	...	...	...
Orthotomus sepium	...	X	O	...	...
Rhipidura perlata	X	...	...	...	...
Muscicapa dumetoria	X	...	...	...	...
Rhinomyias umbratilis	X	...	...	...	...
Hypothymis azurea	...	...	X	...	...
Anthreptes simplex	...	...	X	...	...
Anthreptes rhodolaema	...	...	X	...	...
Nectarinia hypogrammica	...	X	...	...	...
Arachnothera longirostris	...	...	...	...	X
Arachnothera flavigaster	...	...	...	...	X
Arachnothera chrysogenys	...	...	...	...	X
Arachnothera affinis	...	...	...	...	X
Zosterops everetti	...	O	X	...	...
Lonchura fuscans	...	X	O	...	...
Oriolus xanthonotus	...	X	O	...	...
Platysmurus leucopterus	...	X	O	...	...
Total Primary	16	18	14	2	4
Total Secondary	1	8	14	0	0

recorded on mountains the summits of which are lower than 5,000 feet, although on higher peaks the actual lower limit of occurrence may be considerably below 5,000 feet. Montane birds have not been recorded on mountains the summits of which are lower than

3,000 feet, although specimens may have been taken below that altitude on higher peaks. Submontane, as defined by Smythies, is a comprehensive term applied to birds occurring from sea level to an elevation of 5,000 feet but ordinarily not found away from mountainous country. The Lowland birds normally range from sea level to 3,000 feet. Of the 125 species of birds observed at Quoin Hill, 1.6 per cent were Montane, 14.4 per cent were Submontane and 84 per cent were Lowland species. The distribution of birds 12 miles north of Kalabakan closely resembled that at Quoin Hill except for the total absence of Montane species and an increase of Submontane species to 25 per cent. The observation of fewer species (48) can be attributed to the nearly uniform habitat.

The avifauna in the moss forest 5.5 miles southwest of Tenom was unusual in that 45.4 per cent consisted of Lowland species; this locality lies 4,000 feet above sea level, yet only 27.3 per cent of its species were Submontane and 27.3 per cent Montane. If one looks at these figures from the standpoint of the actual importance of the three groups at this place, however, a different picture emerges. Some of the Lowland species were seen only once while I was there and few were common, while all of the Submontane and most of the Montane forms were more or less common.

SEASONALITY OF BREEDING

The breeding season in North Borneo.—Birds in the Quoin Hill area of eastern Borneo seem to breed most commonly in June, July, and August. Table 2 lists 34 of the more common species at Quoin Hill for which evidence on breeding was available. The actual evidence was provided by females with active brood patches or active ovaries, males with enlarged testes, birds in juvenal plumage, or birds actively in annual molt. From such data dates of presumed breeding were extrapolated. In Table 2, the solid black lines indicate dates for which both male and female were in breeding condition. The dotted lines indicate enlarged testes but no evidence of breeding in females. In the bottom line of Table 2, the figures indicate the percentage of the population breeding in any one month. For instance, 2.9 per cent of the birds were breeding in March, but 73 per cent were breeding in June. Rainfall records from the Cocoa Research Station from April, 1959, to December, 1964, were available to me. These data, along with the average for each month, are given in Table 3. There appears to be little correlation between rainfall and breeding season at Quoin Hill.

TABLE 2.—Seasonality of common breeding birds at Quoin Hill. Solid lines indicate times of occurrence of known breeding; dotted lines represent times of presumed breeding.

A true dry season in the Quoin Hill area does not occur, but monthly rainfall has varied from 0.57 inches to 21.27 inches in a single year.

Birds in the moss forest near Tenom appeared to be breeding in January, paralleling the trend found by Voous (1950a) for the lowlands of Borneo.

Other Bornean observations.—Voous (1950a) summarized data assembled by Coomans de Ruiter on the breeding of birds in the lowland of western Borneo near Pontianak. It appears that the

TABLE 3.—Monthly rainfall records, Cocoa Research Station, Quoin Hill.

YEAR	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1959....	.....	.....	.....	6.49	12.16	11.11	7.64	12.11	4.75	8.33	12.10	13.81
1960....	9.24	8.17	3.76	10.65	8.84	11.00	6.31	11.25	8.56	5.49	8.39	11.81
1961....	6.68	8.06	4.35	4.74	7.55	7.25	5.93	2.40	7.47	5.58	4.38	10.73
1962....	3.82	6.76	13.72	9.68	6.82	7.49	6.59	5.82	7.81	9.47	19.80	9.28
1963....	21.27	8.18	7.64	0.57	5.83	4.62	0.64	12.49	5.24	8.75	7.43	11.05
1964....	4.17	7.92	4.40	11.20	11.82	8.04	2.42	7.52	5.69	13.15	8.82	9.88
Average	9.03	7.81	6.77	7.22	8.83	8.25	4.92	8.59	6.58	8.46	10.15	11.09

breeding season in that part of Borneo, and indeed in all of western Borneo (Banks, 1950), starts in December and reaches a peak in March.

Gibson-Hill (1952) has questioned Banks' (1950) interpretation of data from the egg collection of V. W. Ryves. Gibson-Hill has shown that the data collected by Ryves covered two widely separated localities, one at Kiau near Kota Belud and the other near Sandakan. The former locality is on the west coast of North Borneo and the latter on the east coast of North Borneo. Gibson-Hill points out, and rightly so, that the timing of the rainfall in different parts of Borneo must be taken into account because of the large regional variation. The nesting data from the Ryves egg collection are scant and when used alone possibly yield a distorted view of the actual breeding season. Ryves did no collecting in the Sandakan area between September and March, and in the Kiau area between May and January. Although the breeding data from North Borneo accumulated by both Ryves and myself are limited, and records of rainfall are scant, there appears to be a trend toward breeding after the heavy rains have fallen.

Seasonality of breeding in tropical birds.—Possibly Bornean birds breed mostly in the "driest" part of the year. If so, this is in contrast with the time of breeding of birds of other tropical areas. Moreau (1950) found that in the Congo there was no distinct breeding season for most groups of birds, but that in East Africa there was a double breeding season; the peaks coincided with the two rainy seasons. Lack (1950) found that the Geospizinae of the Galapagos breed only when it rains and that rainfall causes a flurry of nest building and singing. If the rains stop, then the courtship activities stop until the next rains. Miller (1963) found that in birds of a western Andean cloud forest the breeding season

was spread over the year and that breeding could not be correlated with rainfall.

Obviously more study is required on breeding of birds in Borneo before the timing of the annual cycle can be ascertained.

ACCOUNTS OF SPECIES

The English names used in this report follow Smythies (1960) where possible. If the bird has not been recorded from Borneo previously, then I have resorted to Delacours and Mayr's "Birds of the Philippines" (1946). The taxonomy is that of Smythies (1960), except where current American or my own opinion differs and where new evidence has warranted a change. The sequence of families is that of Wetmore (1960).

Two species listed beyond that had not previously been recorded from the island of Borneo are: Red-footed Booby, *Sula sula;* and Whitehead's Thick-head, *Pachycephala whiteheadi.* Six additional kinds listed beyond had not previously been recorded from North Borneo. They are: Chinese Egret, *Egretta eulophotes;* Knot, *Calidris canutus;* Ground Cuckoo, *Carpococcyx radiceus; Stachyris nigriceps hartleyi;* Finch's Bulbul, *Criniger finschii;* and Pale Blue Flycatcher, *Muscicapa unicolor.*

Sula sula (Linnaeus): Red-footed Booby.—A captive seen in the Tawau police station was said to have been caught when it landed at night on a police launch anchored off Siamil Island in or near May, 1962. The bird was in first-year or second-year plumage, seemed to be tame, and was thriving on a diet of fish. Identification was made by Alexander Wetmore from a photographic print. This is the first seemingly substantiated record of the species from Borneo, although it probably occurs there regularly. The species breeds on Bankoran Island and on Tubbataha Reef in the Sulu Sea (Smythies, 1960: 113).

Fregata ariel (G. R. Gray): Lesser Frigatebird.—This conspicuous bird on the waters around Tawau is occasionally seen in Cowie Harbor but more often along the coast outside the Harbor. On September 20 an estimated 300-500 birds circled over the shore northeast of Tawau.

Ardea sumatrana sumatrana Raffles: Dusky-gray Heron.—*Specimens,* 2. Karindingen Island: ♂ testis 12 × 23 mm., November 24, 1962, MCT 3308; ♂, November 24, 1962, MCT 3309.

The specimens were taken on the coral sand beach surrounding Karindingen Island. At least 10 were seen feeding on the beach and on a reef. One (MCT 3308) had testes of a size suggesting that it was in breeding condition.

Casmerodius alba modestus (Gray): Common Egret.—*Specimen,* I. Karindingen Island: ♀, November 24, 1962, MCT 3310.

This species was seen on three dates: August 17 at Karindingen Island, where 30 were observed feeding along the mangroves bordering the island; on November 24, on the same island, where a specimen was taken from a flock

of 30 birds that had been feeding on the coral sand and reef; and on November 30 when a single bird landed at the small reservoir at the Cocoa Research Station and began to feed in the shallow water. Only four specimens appear to have been recorded earlier (Smythies, 1957:561), although Smythies (1963: 270) lists additional sight records.

Egretta garzetta (Linnaeus): Little Egret.—On November 24 at Karindingen Island, I observed several mixing freely with individuals of *E. sacra* on the coral sand beaches and reefs.

Egretta eulophotes (Swinhoe): Chinese Egret.—*Specimen,* 1: Ka-Karis, Kinabatangan River, 200 feet: ♂, October 20, 1963, ADG 326.

This is the only record known to me of this species from North Borneo. Smythies (1960:126) lists 11 specimens from other parts of Borneo.

Egretta sacra (Gmelin): Reef Egret.—The species was observed at Karindingen Island on August 17 and November 24, 1962, and was the most common egret on the island. One compact flock of 50 was seen at high tide. No white-phased birds were in the flock.

Bubulcus ibis coromandus (Boddaert): Cattle Egret.—*Specimen,* 1: Tongod: ♀, October 21, 1963, ADG 328.

Individuals were observed daily at Tuaran with cattle at the Agricultural Research Centre. I saw them on December 9 when I arrived at Tuaran and again on January 13, when I departed.

Ardeola bacchus (Bonaparte): Chinese Pond Heron.—*Specimen,* 1: 12 mi. N Kalabakan: ♀, October 26, 1962, MCT 3151.

The specimen was brought to our camp by a local boy who obtained it on a stream that ran through his kampong (village) near our sulap (hut). The stream was a small one that ran out of the primary forest, through the village, and back into secondary forest.

Butorides striatus (Linnaeus): Little Green Heron.—*Specimens,* 2: Telipok: ♀, March 10, 1963, TM 67; Sex?, December 13, 1962, TM 6.

This heron was seen at Karindingen Island on August 17, 1962, in a small swamp near the Tawau airport on September 16, and on the reef at Siamil Island on September 18. The specimens collected at Telipok were not identified to subspecies.

Ixobrychus cinnamomeus cinnamomeus (Gmelin): Chestnut Bittern.—*Specimen,* 1: Tuaran: Sex?, December 24, 1963, SCFC 32.

This specimen was probably taken in the paddy around the Agricultural Research Centre, where I saw Chestnut Bitterns in January 1963.

Leptoptilos javanicus (Horsfield): Lesser Adjutant Stork.—*Specimen,* 1: Karindingen Island: ♂ testis small, November 24, 1962, MCT 3311.

My first observation of this species was at Karindingen Island on August 17, when approximately 100 birds were seen feeding on the coral sand and reefs. I saw them also within a mile of Semporna along the ship channel, usually in the vicinity of fish traps. On August 31 two birds flew high overhead at Quoin Hill, proceeding in the direction of Cowie Harbor. On November 24, large numbers at Karindingen Island were sitting in mangroves and feeding on the reefs around the island. Two birds were caught by the rising tide while feeding on the reef and were unable to take off. One of these was shot in approximately six to seven feet of water; its feathers were completely water-

logged. Interestingly the flaky skin of the crown had blue-green algae growing on it. These birds were heard calling many times on the reef and in the mangroves; the call is much like the deep growl of a dog.

Sims, Banks, and Harrison have found the storks common in this area (Smythies, 1957:569). Although I could find no evidence of it, possibly Karindingen Island is a nesting locality.

Anas querquedula Linnaeus: Garganey.—*Specimen,* 1: Kg. Banjar: sex? November 13, 1963, ADG 329.

This teal obtained by Garcia is our only record of any duck from North Borneo.

Haliastur indus (Boddaert): Brahminy Kite.—This common resident of the Cocoa Research Station was observed almost daily while I was in the field. It seemed to prefer the cleared areas replanted to cocoa and oil palm and was common also at Tawau, Semporna, and Karindingen Island.

Accipiter trivirgatus microstictus Mayr: Crested Goshawk.—*Specimens,* 2: Pintasan Agriculture Station: ♂, October 17, 1963, ADG 314. Cocoa Research Station: ♂, April 30, 1963, ADG 89.

Spizaetus cirrhatus limnaetus (Horsfield): Changeable Hawk-eagle.—*Specimen,* 1: Tiger Estate: ♂, April 28, 1963, ADG 74 (Specimen in black phase).

Hieraetus kienerii formosus (E. Geoffroy): Rufous-bellied Hawk-eagle.—*Specimens,* 2: Cocoa Research Station: ♀ imm., July 10, 1962, MCT 2615. Tiger Estate: ♀, July 13, 1962, MCT 2621.

The presence of an immature bird of this species in North Borneo lends support to the suggestion of Smythies (1957:580) that this species breeds in Borneo.

Haliaeetus leucogaster (Gmelin): White-bellied Sea Eagle.—This eagle appears to be fairly common along the coast in the Tawau-Darvel Bay area. I saw it around Cowie Harbor, Tawau, Semporna, and Siamil Island.

Spilornis cheela Latham: Crested Serpent Eagle.—I saw this eagle but once, circling overhead at the Cocoa Research Station on September 26, 1962.

Microhierax latifrons Sharpe: White-fronted Falconet.—*Specimens,* 2: Cocoa Research Station: ♂ testis 2 × 1 mm., 41.2 gm., July 6, 1962, MCT 2600. Tiger Estate: ♀ oviduct regressing, old brood patch, December 1, 1962, MCT 3418.

This species was first seen at the Cocoa Research Station. The specimen taken there bobbed its head in the manner of various other falcons. On two occasions individuals were observed sitting in a low tree in the front yard of a home in Kalabakan.

These records extend the known range of this species south from Darvel Bay (Smythies, 1960:161) to Cowie Harbor.

Falco peregrinus japonensis Gmelin: Peregrine Falcon.—*Specimen,* 1: Kampong Kuamut: ♂, October 20, 1963, ADG 327.

Coturnix chinensis (Linnaeus): Painted Quail.—*Specimen,* 1: Cocoa Research Station: ♂ testis 8 × 5 mm., September 6, 1962, MCT 2881.

This specimen is intermediate between *C. c. lineata* and *C. c. caerulescens,* tending slightly toward the latter in having more rufous coloring on the tertials.

R. E. Kuntz took a male at Ranau (USNM 472504) that was also intermediate in its characters but was referable to *C. c. lineata*. These two specimens, when compared with series of specimens from the Philippines and Sumatra, fitted into a clinal progression of increasingly rufous tertials toward Sumatra. Peters (1934:96) united *C. c. caerulescens* with *C. c. palmeri*, but Amadon (in *litt.*) retains *C. c. caerulescens* (Smythies, 1957:588). No clear-cut distributional pattern is yet discernible in North Borneo and the arrangement of Amadon (MS) should probably be reviewed again when more specimens become available.

These birds were observed several times at the Cocoa Research Station but were difficult to collect. They were abundant in the grasslands on the Brantian Estate.

Rollulus roulroul (Scopoli): Crested Green Wood Partridge.—It was observed once along the Apas River at the Cocoa Research Station, in primary forest.

Haematortyx sanguiniceps Sharpe: Crimson-headed Wood Partridge.—Frederick Dunn saw one fly across the padang at the Cocoa Research Station rest house on September 9.

Lophura ignita (Shaw and Nodder): Crested Fireback Pheasant.—*Specimens,* 3: Cocoa Research Station: ♀, molting, July 20, 1962, MCT 2624. 12 mi. N Kalabakan: ♀, November 4, 1962, MCT 3206; ♂, November 7, 1962, MCT 3216.

This pheasant was taken in native snares from primary forest.

Lophura bulweri (Sharpe): Bulwer's Pheasant.—*Specimens,* 3: 5.5 mi. SW Tenom: ♀, December 25, 1962, MCT 3534; ♂, December 27, 1962, MCT 3539; ♀, December 27, 1962, MCT 3540.

This bird was first taken in a snare 12 miles north of Kalabakan. Unfortunately, the specimen was stolen and only its tail feathers were brought in by the trappers. Mr. Comber of Sapong Estates in Tenom said this species comes in numbers with the wild-pig migration and that he had observed this at least three times. He has also seen three-quarters grown young at Tenom, so they seemingly nest there. They were found only in primary forest.

These specimens constitute the first records of the species for the west coast of North Borneo (*cf.* Smythies, 1957:593).

Argusianus argus grayi (Elliott): Great Argus Pheasant.—*Specimens,* 6: 12 mi. N Kalabakan: ♂, October 14, 1962, MCT 3034; ♀, October 22, 1962, MCT 3121; ♂, October 23, 1962, MCT 3130; ♂, October 27, 1962, MCT 3166; ♀?, October 29, 1962, MCT 3307. 5.5 mi. SW Tenom: ♀, December 19, 1962, MCT 3464.

This species is a common resident of the primary forest at Kalabakan and in the lower areas around Tenom (J. A. Comber, pers. comm.). It is found only in primary forest.

Rallina fasciata (Raffles): Malaysian Banded Crake.—*Specimen,* 1: Tiger Estate: ♂, July 11, 1963, ADG 193.

Amaurornis phoenicurus javanicus (Horsfield): White-breasted Waterhen.—*Specimens,* 3: Tuaran: sex?, March 1, 1963, ADG 5. Telipok: ♀, February 2, 1963, TM 23; ♂, February 2, 1963, TM 24.

This species was commonly observed in marshes near Tawau and on the Brantian Estate.

Gallicrex cinerea (Gmelin): Watercock.—*Specimen,* 1: Tiger Estate: sex?, December 17, 1962 (taken on dry grassland).

Squatarola squatarola (Linneaus): Black-bellied Plover.—On September 2 I saw a flock of 12 plovers on the Tawau golf course. They were in a mottled plumage indicating extensive molt and feather growth. Later in the day a bird in almost complete breeding plumage flew overhead.

Charadrius peroni Schlegel: Malay Sand Plover.—On September 15, one was sitting on the Tawau Airport runway. Another was observed on November 20, feeding near a water buffalo wallow on the Brantian Estate. Smythies (1960:191) lists sandy beaches as the only habitat.

Charadrius leschenaulti Lesson: Large Sand Plover.—On September 16 one was sitting on the Tawau Airport runway.

Numenius phaeopus variegatus (Scopoli): Whimbrel.—*Specimen,* 1: Karindingen Island: ♂, November 24, 1962, MCT 3315.

This was the most common curlew around Karindingen Island on November 24. Flocks of 10 to 20 individuals were feeding on the coral sand around the island, and a few individuals were sitting in the tops of dead mangroves at low tide.

Numenius arquata (Linnaeus): Common Curlew.—On November 24, a Common Curlew flew from Karindingen Island toward the mainland.

Numenius madagascariensis (Linnaeus): Eastern Curlew.—I first observed this curlew on August 17 at Karindingen Island, where 50 were feeding on the coral sand. At that time it was the most abundant shorebird. When I returned to the island on November 24, several were seen around the island, but the species was not so abundant as *N. phaeopus.*

Limosa lapponica (Linnaeus): Bar-tailed Godwit.—A flock of five was observed at Karindingen Island on November 24.

Tringa totanus eurhinus (Oberholser): Redshank.—*Specimens,* 2: Karindingen Island: ♀, November 24, 1962, MCT 3312; ♀, November 24, 1962, MCT 3313.

On August 17, this bird was common and feeding on the coral sand at Karindingen Island. When I revisited the island on November 24 the Redshank seemed to prefer the mangrove areas for feeding and was the most common wader.

Tringa ochropus Linnaeus: Green Sandpiper.—*Specimen,* 1: Brantian Estate: ♀, November 19, 1962, MCT 3305.

The specimen, one of three or four birds seen, was taken near a grassland pond.

Heteroscelus incanum (Gmelin): Wandering Tattler.—One was feeding along a sandy beach and later on rocks on Siamil Island on September 18, 1962.

Capella megala (Swinhoe): Swinhoe's Snipe.—*Specimens,* 3: Tiger Estate: sex?, December 9, 1962; sex?, December 9, 1962. Pintasan Agriculture Station: ♂, October 17, 1963, ADG 317.

These three specimens lend support to the theory of Smythies (1960:206) that this species is the common snipe of North Borneo.

Calidris canutus (Linnaeus): Knot.—On August 17, I saw 20 Knots feeding on the coral sand at Karindingen Island. They were still partly in breeding feather, showing rusty color here and there on the breast. I saw no Knots on

November 24 at Karindingen Island. There is but one prior record for Borneo, from the North Natuna Islands (Chasen, 1935:39).

Erolia ruficollis (Pallas): Red-necked Stint.—*Specimen,* 1: Karindingen Island: ♂, November 24, 1962, MCT 3314.

The species was common on November 24 around Karindingen Island, usually in flocks of 5 to 10 birds.

Glareola pratincola (Linnaeus): Collared Pratincole.—*Specimen,* 1: Tiger Estate: ♂, April 28, 1963, ADG 75.

Chlidonias hybrida (Pallas): Whiskered Tern.—*Specimen,* 1: Kuala Sumawang: sex?, September 18, 1962, ADG 280.

Smythies (1960:217) lists no record for North Borneo.

Sterna bergii Lichtenstein: Greater Crested Tern.—*Specimens,* 2: Kuala Sumawang: ♀, September 18, 1963, ADG 278; ♂, September 18, 1963, ADG 279.

This tern was observed several times off the coast of North Borneo near Tawau.

Treron curvirostra curvirostra (Gmelin): Thick-billed Pigeon.—*Specimens,* 9: Cocoa Research Station: ♂ testis 9 × 5 mm., 166.7 gm., August 1, 1962, MCT 2693; ♂ testis 5 × 4 mm., 167.2 gm., August 1, 1962, MCT 2694; ♂ testis 13 × 6 mm., 167.8 gm., August 1, 1962, MCT 2695; ♂ testis 9 × 5 mm., 155.5 gm., August 1, 1962, MCT 2700; ♀, 112.9 gm., August 2, 1962, MCT 2712; ♂, 185.8 gm., August 2, 1962, MCT 2713; ♀, 135.4 gm., growing new 5th primary, August 25, 1962, MCT 2806; ♀, 132.2 gm., August 31, 1962, MCT 2842; ♂, 112.5 gm., August 31, 1962, MCT 2843.

This pigeon was the most common bird eating wild figs (*Ficus*) in the communal feeding trees, where there were as many as 30 gathered in one tree to feed. While resting, individual birds commonly dipped their tails.

Treron olax olax (Temminck): Little Green Pigeon.—*Specimens,* 2: Cocoa Research Station: ♂ testis 11 × 5 mm., September 1, 1962, MCT 2844. Pintasan Agriculture Station: ♂, October 14, 1963, ADG 306.

The species was seen only once. At the Cocoa Research Station, one bird sat on a dead tree and fed on a red berry from a vine. The call resembled the crying of a child. Others called in the cocoa. The bird taken had testes of a size indicating possible breeding condition.

Treron vernans purpurea (Gmelin): Pink-necked Green Pigeon.—*Specimens,* 10: Tiger Estate: ♂, November 25, 1962, MCT 3323; ♀, November 25, 1962, MCT 3325. Telipok: ♀, January 31, 1963, TM 22; ♀, January 31, 1963, TM 20; ♂, January 31, 1963, TM 19; ♀, January 31, 1963, TM 21; ♂, February 10, 1963, TM 35; ♂, February 2, 1963, TM 25. Mt. Rumas: ♀, March 6, 1963, ADG 11. Tuaran: ♀, November 29, 1963, SCFC 34.

The species was confined to the lowlands around Tawau, as at the Tawau Airport in the scrub growth. Flocks of 50 to 100 were observed at Tuaran. None of the specimens taken in November was in breeding condition.

Ducula bicolor (Scopoli): Pied Imperial Pigeon.—I observed this pigeon on September 18 and 19 at Siamil Island. On the first day two were seen in the few remaining trees on the island and on September 19 a flock of 12 flew southwest over the island at about 8:30 A. M.

Streptopelia bitorquata (Temminck): Javanese Turtle Dove.—On Siamil Island on September 18 and 19, two were seen at close range feeding with

10 S. *chinensis*. There is only one other record from Borneo; Pryer took one at Sandakan in the 1880's (Everett, 1889:193) and it has not been recorded since. Chasen (1935:22) speculated that the Javanese Turtle Dove was introduced to Borneo as a cage bird. But, Borneo is seemingly well within the normal range of the species and probably it is a resident of North Borneo. The Javanese Turtle Dove and the Spotted-necked Dove, S. *chinensis*, closely resemble each other; this resemblance may help to account for the lack of records of S. *bitorquata*.

Streptopelia chinensis (Scopoli): Spotted-necked Dove.—*Specimens*, 2: Tiger Estate: ♂, June 19, 1963, ADG 149. Telipok: ♂, February 10, 1963, TM 34.

This is a common bird of the coconut groves around Tawau and on Siamil Island.

Chalcophaps indica (Linnaeus): Emerald Dove.—*Specimen*, 1: Cocoa Research Station: ♂, June 17, 1963, ADG 146.

Birds, always solitary, of this species often were seen in the cocoa groves at the Cocoa Research Station.

Tanygnathus lucionensis lucionensis (Linnaeus): Blue-naped Parrot.—*Specimens*, 3: Siamil Island: ♂, September 19, 1962, MCT 2928; ♀, September 19, 1962, MCT 2929; ♀, September 19, 1962, MCT 2930.

These birds were seen on September 18 and 19. I saw flocks of 10 to 20 in the remnant of forest on the north side of the island. The birds were almost entirely inhabitants of the forest and were rarely seen in the coconut groves. I estimated the entire island population to be between 30 and 100 birds. The Japanese residents knew nothing of the birds, although they were aware of a cockatoo (*Cacatua galerita*) that had lived at large on the island for several years. The Blue-naped Parrot has been found only on the Maratuas and on Mantanani Island. Smythies (1960:242) surmised that the Mantanani population was introduced by sailing craft from the Sulu Sea. In the light of the present discovery, I think the species is a naturally-established resident of the North Bornean islands.

Psittinus cyanurus cyanurus (Forester): Little Malay Parrot.—*Specimens*, 2: Tiger Estate: ♀, October 11, 1962, MCT 2998; ♂, October 11, 1962, MCT 2997.

Smythies (1963:277) was the first to record this species from North Borneo. However, the Harvard Primate Expedition in 1938 took three specimens as follows: ♂, Sandakan, June 6, 1937, MCZ 197123; ♂, Morutai Besar, June 27, 1937, MCZ 197124; ♂, Kalabakan River, July 16, 1937, MCZ 197125. The Harvard collection of birds from North Borneo appears to have been overlooked, although it was mentioned in passing by Smythies (1960:526). The specimens in my collection were taken in the same general area where H. G. Deignan took the Harvard specimens.

Loriculus galgulus (Linnaeus): Malay Lorikeet.—*Specimen*, 1: Cocoa Research Station: ♀, May 1, 1963, ADG 103.

This lorikeet was rare at all of our collecting localities.

Cuculus fugax fugax Horsfield: Malayan Hawk-Cuckoo.—*Specimens*, 3: Cocoa Research Station: ♂, 86.0 gm., August 28, 1963, MCT 2825; ♂, 79.0 gm., September 11, 1962, MCT 2899; ♀, September 28, 1962, MCT 2977.

This species was first observed on August 28 in primary forest and was seen regularly from then until September 28 in secondary forest, primary forest, and in cocoa shade trees.

Cacomantis sonnerati (Latham): Banded Bay Cuckoo.—Birds that may have been of this species were observed on several occasions. E. J. H. Berwick (pers. comm.) claimed he had heard *C. sonnerati* at the Cocoa Research Station. I have heard many times a call sometimes ascribed to this species but I have not actually seen the bird making the sound. If the call note I heard is actually of this species it is not rare in the Quoin Hill area.

Cacomantis merulinus threnodes Cabanis and Heine: Plaintive Cuckoo.—*Specimens,* 5: Cocoa Research Station: ♂, 25.0 gm., September 8, 1962, MCT 2891; ♀ imm., 27.0 gm., September 8, 1962, MCT 2892; ♂ testis 4 × 3 mm., November 29, 1962, MCT 3382. Tenom: ♂, January 1, 1963, MCT 3563. Ulu Balung: ♀, July 15, 1963, ADG 199.

This cuckoo was common in all habitats examined at all of our collecting stations, except the moss forest near Tenom.

Cacomantis variolosus sepulchralis (S. Muller): Fantailed Cuckoo.—*Specimens,* 2: Cocoa Research Station: ♂, 30.8 gm., August 28, 1962, MCT 2824. Ulu Balung: ♂, July 10, 1963, ADG 183.

The specimens were collected in primary forest. There are only five earlier records for all of Borneo (Smythies, 1960:253-254). Probably this species nests in Borneo; it is unlikely that specimens taken in August and July are migrants.

Chalcites xanthorhynchus xanthorhynchus (Horsfield): Violet Cuckoo.—*Specimens,* 1: Cocoa Research Station: ♀ largest ovum 1 mm., September 26, 1962, MCT 2964.

This species was seen twice, both times in the research station cocoa plantings. The specimen taken was from a shade tree, *Trema orientalis.*

Chalcites malayanus aheneus Junge: Malaysian Green Cuckoo.—*Specimens,* 9: Cocoa Research Station: ♀ definite brood patch, 17.5 gm., body molt, July 4, 1962, MCT 2587; ♂ testis 4 × 4 mm., 19.1 gm., August 8, 1962, MCT 2736; ♀, 17.5 gm., August 8, 1962, MCT 2737; ♂, 17.5 gm., August 8, 1962, MCT 2738; ♂ testis 4 × 3 mm., 18.2 gm., August 8, 1962, MCT 2739; ♀, August 25, 1962, MCT 2809; ♂, 21.1 gm., September 11, 1962, MCT 2900; ♂, October 2, 1962, MCT 2984. Tiger Estate: ♀ oviduct enlarged, brood patch, November 25, 1962, MCT 3318.

This cuckoo was common in the cocoa planting at the Cocoa Research Station and not found in any other type of habitat. Smythies (1960:255) thought that possibly two species of *Chalcites* were represented in the series of *Chalcites malayanus* from Borneo. I have assembled all 20 known specimens, however, including seven in the Museum of Comparative Zoology at Harvard unreported by Smythies (1957:638) and find that the variation in the coloration of the head and upperparts is due to the difference in sexes, the males being darker than the females. There is much variation in the length of the wing, but the meaning of this variation is not yet clear.

Surniculus lugubris barussarum (Oberholser): Drongo-cuckoo.—*Specimens,* 2: Cocoa Research Station: ♀ imm., July 28, 1962, MCT 2672, discarded; ♀ imm., 28.6 gm., August 25, 1962, MCT 2810.

The first specimen was taken in secondary forest; it had been sitting in a

dead tree, occasionally darting out after insects. The second specimen was taken in cocoa; its stomach contained 50 caterpillars.

Eudynamys scolopacea (Linnaeus): Koel.—This species was observed at Tawau and on Siamil Island, on August 30 and September 18, respectively.

Clamator coromandus (Linnaeus): Red-winged Crested Cuckoo.—*Specimen,* 1: Telipok: ♀, February 10, 1963, TM 33.

Phaenicophaeus chlorophaeus fuscigularis (Baker): Raffles Malcoha.—*Specimen,* 1: Cocoa Research Station: ♂, August 26, 1962, MCT 2813.

Flocks of three and four were seen in the cocoa. At Kalabakan the species was feeding about 40 feet up in the second canopy layer of the primary forest.

Phaenicophaeus diardi borneensis (Salvadori): Lesser Green-billed Malcoha.—*Specimens,* 3: Cocoa Research Station: ♀, 58.2 gm., July 22, 1962, MCT 2636; ♀, 55.8 gm., September 8, 1962, MCT 2890; ♂, September 13, 1962, MCT 2918.

This malcoha was seen only three times; it was the second most common malcoha.

Phaenicophaeus javanicus pallidus (Robinson and Kloss): Red-billed Malcoha.—*Specimens,* 2: Cocoa Research Station: ♀, 97.0 gm., August 31, 1962, MCT 2841; ♂, 98.0 gm., September 8, 1962, MCT 2889.

The two specimens were taken in cocoa. On October 2, 1962, I saw one about 100 feet up in the top canopy layer of the primary forest at the Cocoa Research Station and, on October 3, two more hopping from branch to branch about 150 feet up in a tree.

Phaenicophaeus curvirostris borneensis (Blasius and Nehrkorn): Chestnut-breasted Malcoha.—*Specimens,* 7: Cocoa Research Station: ♀ old brood patch, 121.8 gm., July 6, 1962, MCT 2602; ♀, September 4, 1962, MCT 2864; ♂ testis 3 × 2 mm., 143.6 gm., wing molt, July 7, 1962, MCT 2611; ♂ testis 6 × 2 mm., 111.0 gm., August 11, 1962, MCT 2763; ♀, May 25, 1963, ADG 110. Ulu Balung: sex?, July 24, 1963, ADG 216. Tiger Estate: ♂, June 22, 1963, ADG 156.

This was the most numerous of the malcohas at the Cocoa Research Station. It was observed in primary forest, secondary forest, citrus trees, and cocoa trees. In the primary forest it ranged in the upper canopy from 100 to 150 feet up.

As Peters has indicated (1940:56), the name *P. c. borneensis* (Blasius and Nehrkorn) 1881 has priority over *P. c. microrhinus* Berlepsch 1895 (used by Smythies).

Centropus sinensis (Stephens): Common Coucal.—*Specimen,* 1: Cocoa Research Station: ♀, May 15, 1963, ADG 108.

The finding of a coucal at the Cocoa Research Station on May 15, 1963, came as something of a surprise, since none had been seen there earlier by our group. Coucals were seen at Tawau but were not collected or identified to species.

Centropus bengalensis (Gmelin): Lesser Coucal.—*Specimens,* 2: Tuaran: ♀, April 1, 1963, ADG 46; sex?, December 3, 1963, SCFC 17.

Carpococcyx radiceus radiceus (Temminck): Ground Cuckoo.—*Specimen,* 1: 12 mi. N Kalabakan: ♂ imm., November 7, 1962, MCT 3217.

This male was taken in a native snare in primary forest and provides our only record. The specimen is in the postjuvenal (first prebasic) molt.

This record is the first for this species from North Borneo (Smythies, 1957: 643); others are known from Sarawak and Indonesian Borneo.

Otus bakkamoena lemurum Deignan. Collared Scops Owl.—*Specimens*, 3: Tiger Estate: ♀, November 25, 1962, MCT 3319. Tenom: ♂ testis 6 × 5 mm., body molt, January 1, 1963, MCT 3552. Agricultural Oil Palm Station: ♂, October 6, 1963, ADG 299.

The specimen from Tenom was taken in a bird net set in a grass-scrubland situation; the testes were regressing. Harrison (Smythies, 1957:645) found this species breeding in the Kelabit uplands in January.

Glaucidium brodiei borneense Sharpe: Pygmy Owlet.—*Specimen*, 1: Ulu Balung: ♂, July 19, 1963, ADG 210.

The specimen taken by Garcia is the sixth known (Smythies, 1957:646) from Borneo and the first from the east coast. Specimens were collected in 1956 in North Borneo by the Cambridge Expedition.

Ninox scutulata borneensis (Bonaparte): Hawk-owl.—*Specimen*, 1: Tenom: ♀ largest ovum 2 mm., oviduct evident, January 6, 1963, MCT 3583.

This female, taken in a bird net in a grass-scrubland association, was coming into breeding condition.

Strix leptogrammica Temminck: Malaysian Wood Owl.—*Specimens*, 2: Cocoa Research Station: sex?, July 9, 1963, ADG 182; ♂, May 25, 1963, ADG 111.

On September 7, 1962, I flushed two of these owls from a tree beside the Apas River in primary forest. One was subsequently shot but lost. Garcia's two specimens were not identified to subspecies.

Caprimulgus macrurus salvadori Sharpe: Long-tailed Nightjar.—*Specimens*, 3: Tuaran: ♀, January 12, 1963, MCT 3592; ♀, March 2, 1963, ADG 6. Mt. Rumas: ♂, March 6, 1963, ADG 13.

This was an abundant bird on the Jesselton-Tuaran road but was not seen at any of the other collecting stations in North Borneo.

Collocalia fuciphaga natunae Stresemann: Thunberg Swiftlet.—*Specimens*, 3: Cocoa Research Station: ♀ largest ovum 7 mm., oviduct enlarged, 13.1 gm., June 30, 1962, MCT 2570; ♀ ovary small, September 8, 1962, MCT 2887. 5.5 mi. SW Tenom: ♀, December 20, 1962, MCT 3485.

This swiftlet was seen every day while we were at the Cocoa Research Station and was common also in the mountains around Tenom, where it flew in and out of the fog over our camp.

Collocalia esculenta ssp.: White-bellied Swiftlet.—*Specimens*, 7: Cocoa Research Station: ♂, 5.5 gm., July 4, 1962, MCT 2591; ♂, 6.2 gm., July 5, 1962, MCT 2594; ♂, 6.2 gm., July 1, 1962, MCT 2574; ♀, 6.0 gm., July 4, 1962, MCT 2589; ♀, 5.7 gm., July 4, 1962, MCT 2590. 12 mi. N Kalabakan: ♂ testis 4 × 2 mm., November 10, 1962, MCT 3236; ♂, November 10, 1962, MCT 3237.

This was the most abundant of all the swifts at the Cocoa Research Station and in the Kalabakan area and was seen also at Semporna on August 16, 1962, in a small coral cave near the District Officer's house. This cave was 10 feet high at most, but averaged five to six feet. It harbored about 1,000 birds, most of them nesting back in the dimly lit zone but one small group of 50 nested in the entrance in bright light. The adults were still feeding young, although the latter could fly strongly.

Chaetura leucopygialis (Blyth): White-rumped Spine-tailed Swift.—*Specimens,* 12: Cocoa Research Station: ♀ well-developed brood patch, June 28, 1962, MCT 2565; ♀, 12.9 gm., June 30, 1962, MCT 2567; ♀, June 30, 1962, heavy molt on body, head, wing, tail, MCT 2568; ♀, 14.5 gm., June 30, 1962, MCT 2569; ♀, 13.0 gm., June 30, 1962, MCT 2571; ♀, 13.0 gm., July 1, 1962, MCT 2572; ♂ testis 4 × 2 mm., 12.3 gm., July 1, 1962, MCT 2575; ♂ testis 2 × 1 mm., 14.9 gm., July 2, 1962, MCT 2576; ♀, 15.4 gm., July 5, 1962, MCT 2595; ♂ testis 2 × 1 mm., 15.4 gm., wing molt, July 5, 1962, MCT 2596; ♂ testis 2 × 1 mm., 11.9 gm., July 6, 1962, MCT 2598; ♀, 13.0 gm., July 6, 1962, MCT 2599.

This species was common around the Cocoa Research Station but was not seen elsewhere. There is some variation in color within the populations.

Hemiprocne comata comata (Temminck): White-whiskered Tree Swift.—*Specimens,* 3: Cocoa Research Station: ♂ testis 2 × 1 mm., 17.0 gm., July 28, 1962, MCT 2675; sex?, young in juvenal plumage, MCT 2812; ♂, April 28, 1963, ADG 76.

At the Cocoa Research Station this common bird usually was seen sitting on a dead branch of a shade tree in the cocoa whence it would dart out after insects. It rarely perched higher than 12 feet. Occasionally it was seen in a clearing in the primary forest.

Hemiprocne longipennis longipennis (Rafinesque): Crested Tree Swift.—*Specimens,* 2: Cocoa Research Station: ♂ testis 4 × 3 mm., September 4, 1962, MCT 2866; sex?, 42.8 gm., September 8, 1962, MCT 2888.

These swifts also were common at the Cocoa Research Station. Unlike *H. comata,* these birds flew high and sat far up in trees while resting. I never observed them in the primary forest.

The two specimens were more greenish-blue dorsally than typical *H. l. longipennis.* Specimens from Java were paler gray ventrally and their tertials were more nearly white. Too few specimens were available to permit determination of the constancy of the mentioned variation and the two from the station are referred to the nominate subspecies until more material becomes available.

Harpactes diardi diardi (Temminck): Diard's Trogon.—*Specimens,* 8: Cocoa Research Station: ♀, 95.9 gm., July 2, 1962, MCT 2579; 3 alcoholic naked young, July 3, 1962, presumed young of 2579, MCT 2581-83; ♀, 95.0 gm., August 20, 1962, MCT 2782; ♂ testis 6 × 3 mm., September 5, 1962, MCT 2870; ♂, September 5, 1962, MCT 2871; ♂, December 1, 1962, MCT 3409.

This was the most numerous of the trogons at the Cocoa Research Station. One female was taken in a live trap set for rats in the cocoa. The next day a laborer found a young, presumably of that female, in a nest in the same area. On August 20, a flock of 5 to 10 birds was seen moving together in a loose group through the jungle. This species appeared to be a bird of the primary forest, but occasionally was found in the cocoa.

Harpactes kasumba impavidus (Chasen and Kloss): Red-naped Trogon.—*Specimens,* 2: Cocoa Research Station: ♂, 72.1 gm., August 5, 1962, MCT 3730 (discarded); ♀, September 7, 1962, MCT 2883.

This species of the deep forest was not seen in any other habitat.

Harpactes duvaucelli (Temminck): Scarlet-rumped Trogon.—*Specimens,* 7: Cocoa Research Station: ♀, 30.9 gm., July 24, 1962, MCT 2648; ♂?, December 1, 1962, MCT 3407; ♂, December 1, 1962, MCT 3408. Ulu Balung:

♀, July 18, 1963, ADG 209; ♂, July 18, 1963, ADG 208. Kinabatangan Agricultural Station: ♀, October 13, 1963, ADG 305. 12 mi. N Kalabakan: ♀, October 10, 1962, MCT 2996.

This trogon of the primary forest was second in abundance only to *H. diardi.*

Halcyon concreta (Temminck): Chestnut-collared Kingfisher.—*Specimens,* 2: 12 mi. N Kalabakan: ♂, November 8, 1962, MCT 3222; ♀, November 8, 1962, MCT 3223.

This kingfisher was netted near a small stream in the deep primary forest. Another individual was obtained in moss forest at an elevation of 4,000 feet at Tenom, but was discarded.

Halcyon chloris chloroptera (Oberholser): White-collared Kingfisher.—*Specimens,* 4: 9.5 mi. E Tawau: ♀ largest ovum 3 mm., 61.7 gm., July 29, 1962, MCT 2683; ♂ testis 5 × 4 mm., 60.3 gm., July 29, 1962, paired with 2683. Telipok: ♀, February 9, 1963, G. R. Conway; ♀, February 10, 1963, G. R. Conway.

This is a bird of the sea coast. It was seen at Tawau, Siamil Island, and Karindingen Island.

Halcyon sancta sancta (Vigors and Horsfield): Sacred Kingfisher.—*Specimen,* 1: Cocoa Research Station: ♂, June 17, 1963, ADG 147.

The specimen was taken along the Apas River in scrubland near the river. One previously was recorded from North Borneo, this from Labuan (Smythies, 1957:660). He (1963:278) saw another at Bauto on the Labuk River.

Halcyon pileata (Boddaert): Black-capped Kingfisher.—*Specimens,* 3: Tenom: ♂, January 1, 1963, MCT 3564. Pintasan Agriculture Station: ♀, October 18, 1963, ADG 322; ♂, October 11, 1963, ADG 301.

The specimen from Tenom was caught in a net in the scrub-grassland association. The others were taken along the Kinabatangan River.

Pelargopsis capensis fraseri Sharpe: Stork-billed Kingfisher.—*Specimens,* 2: Telipok: ♂, February 9, 1963, TM 30. Mt. Rumas: ♂, April 16, 1963, ADG 53.

This species was common along the lower reaches of the Kalabakan and Brantian rivers and in the mangroves near Tawau.

Alcedo atthis bengalensis Gmelin: Common Kingfisher.—*Specimen,* 1: Pintasan Agriculture Station: ♀, October 12, 1963, ADG 304.

I saw this kingfisher once along the Apas River at Quoin Hill and again along the beach at Siamil Island.

Alcedo euryzona euryzona Temminck: Blue-banded Kingfisher.—*Specimens,* 4: Cocoa Research Station: ♂, September 7, 1962, MCT 2884. 12 mi. N Kalabakan: ♂, October 19, 1962, MCT 3091; ♀, October 20, 1962, MCT 3099; ♂, October 20, 1962, MCT 3101.

This species was fairly common along streams deep in the primary forest at Quoin Hill.

Ceyx erithacus ssp. (Linnaeus): Forest Kingfisher.—*Specimens,* 4: Cocoa Research Station: ♂, 13.2 gm., September 14, 1962, MCT 2924; 12 mi. N Kalabakan: ♂, October 18, 1962, MCT 3075; ♀, October 26, 1962, MCT 3163. Oil Palm Research Station: ♂, September 5, 1963, ADG 273.

All specimens taken showed characters intermediate between those of the subspecies *C. e. motleyi* and *C. e. rufidorsus.* Voous (1951) states that, in all the Malaysian region, the greatest number of hybrids between these two sub-

species occurred in Borneo and, further, that he could find hybrid specimens showing practically all imaginable character combinations. My specimens also showed these intermediate tendencies and I am unable at present to allocate the specimens to subspecies.

Merops viridis viridis Linnaeus: Blue-throated Bee-eater.—*Specimens,* 9: Mt. Rumas: ♂, March 5, 1963, ADG 9; ♂, March 5, 1963, ADG 10; ♀, March 6, 1963, ADG 20; ♂, March 7, 1963, ADG 21; ♀, March 7, 1963, ADG 22; ♂, March 7, 1963, ADG 23. Telipok: ♀, March 24, 1963; ADG 39. Pintasan: ♂, October 22, 1963, ADG 302; ♀, October 12, 1963, ADG 303.

These specimens were all taken in March and October and seem to support Smythies' (1957:664) idea that they arrive with the northeast monsoon (October to March) and are absent the rest of the year.

Nyctiornis amicta (Temminck): Red-bearded Bee-eater.—*Specimen,* 1: Cocoa Research Station: ♂, September 27, 1962, molting, MCT 2970.

The specimen was taken along a stream in the deep primary forest, where it was sitting on a dead twig overlooking the stream. The call note was much like that of a scolding squirrel. This was the only time this species was observed in the Quoin Hill area.

Eurystomus orientalis cyanicollis Vieillot: Broad-billed Roller.—*Specimens,* 4: Cocoa Research Station: ♂ testis 2 × 1 mm., 157.4 gm., heavy molt, July 3, 1962, MCT 2585; ♂ testis 2 × 1 mm., 152.0 gm., heavy molt, July 21, 1962, MCT 2633; ♀, 146.4 gm., heavy molt, July 21, 1962, MCT 2634; ♀, April 29, 1963, ADG 83.

At the Cocoa Research Station this common bird perched in dead trees in the cocoa. On several evenings in September, an individual was seen catching insects in flight at dusk, repeatedly returning to a stump between forays. This continued until it was so dark that I could barely discern the bird.

Berenicornis comatus (Raffles): White-crested Hornbill.—A pair was seen feeding about 150 feet up in a tree at the Cocoa Research Station. No other was seen in northern Borneo.

Annorrhinus galeritus (Temminck): Bushy-crested Hornbill.—This hornbill was seen only on October 3, 1962, at the Cocoa Research Station, when a flock of five flew overhead.

Aceros leucocephalus (Vieillot): Wrinkled Hornbill.—On October 3, 1962, a pair was seen in the primary forest at the Cocoa Research Station.

Aceros undulatus undulatus (Shaw): Wreathed Hornbill.—*Specimens,* 2: Cocoa Research Station: ♀ largest ovum 5 mm., October 2, 1962, MCT 2981; ♂ testis 10 × 11 mm., October 2, 1962, MCT 2982.

This, the most common hornbill at Quoin Hill and at Kalabakan, occurred in primary forest.

Anthracoceros malayanus (Raffles): Black Hornbill.—A flock of five was seen at the Cocoa Research Station rest house on September 6 and 13, 1962.

Buceros rhinoceros Linnaeus: Rhinoceros Hornbill.—It was fairly common at the Cocoa Research Station, where several were observed in July and August.

Rhinoplax vigil (Forster): Helmeted Hornbill.—The Helmeted Hornbill was rarely observed, but almost every day we heard its call when we were on the east coast. It was also heard in the forest on the west coast around

Tenom, but is not common there owing to hunting by the natives. Skulls of this and the preceding species were on sale in a shop at Tenom, despite laws prohibiting the killing of these species.

Calorhamphus fuliginosus tertius Chasen and Kloss: Brown Barbet.—*Specimens,* 7: Cocoa Research Station: ♀ largest ovum 2 mm., 38.8 gm., brood patch, July 7, 1962, MCT 2610; ♀, 40.0 gm., August 1, 1962, MCT 2702; ♀, 44.8 gm., August 1, 1962, MCT 2703; ♂ testis 5 × 3 mm., September 25, 1962 (paired with MCT 2956), MCT 2955; ♀, September 1, 1962, MCT 2846, ♀, September 25, 1962, MCT 2956; ♀ ?, November 30, 1962, MCT 3436.

These barbets were common at the Cocoa Research Station both in secondary forest and cocoa, usually in groups of three or four. They were seen also at Kalabakan where the birds fed in the top of a 100-foot tree in the primary forest.

In describing this bird, Smythies (1960:322) said the male's bill is black. The one male that I took had an orange bill and at no time did I observe any black-billed birds at the Cocoa Research Station; this black bill perhaps is a character of the subspecies *C. f. fuliginosus.*

Megalaima henrici brachyrhyncha Neumann: Yellow-crowned Barbet.—*Specimens,* 3: Cocoa Research Station: ♀, 72.8 gm., August 1, 1962, MCT 2696; ♂ testis 5 × 4 mm., 83.2 gm., August 2, 1962, MCT 2705; ♂ testis 6 × 5 mm., 73.7 gm., August 2, 1962, MCT 2706.

This barbet was common at the Cocoa Research Station and its call could be heard at any time of day until dusk. Smythies (1960:324) described this call as *took-took-took-took-trrrroook.* All birds of this species that I watched and listened to, however, were calling thus: *trrrroook-took-took-took-took.* The number of *tooks* varies, but is generally four and can be as high as seven. This species was heard at all stations on the east coast. At Kalabakan, one was heard calling all day long from the top of a 70-foot tree.

Comparison of my specimens with those in the U. S. National Museum revealed that *M. h. brachyrhyncha* was readily distinguishable from the nominate race by measurements. The average length of bill in my specimens was 23 mm., whereas the average length in two specimens from Sumatra and Siam in the U. S. National Museum was 27 mm. The Bornean specimens differ also in having the blue patch on the head larger and darker than in *M. h. henrici. M. h. brachyrhyncha* certainly seems to be a valid race on the basis of the available specimens.

Megalaima chrysopogon chrysopsis Goffin: Gold-whiskered Barbet.—*Specimens,* 10: Cocoa Research Station: ♀ largest ovum 2 mm., 164.4 gm., July 21, 1962, MCT 2627; ♂ testis 6 × 3 mm., 156.0 gm., August 1, 1962, MCT 2697; ♀, 177.2 gm., August 1, 1962, MCT 2701; ♂ testis 3 × 2 mm., 172.6 gm., August 2, 1962, MCT 2717; ?, 182.2 gm., August 2, 1962, MCT 2718; ♀, 181.5 gm., MCT 2721; ♂ testis 10 × 8 mm., 148.5 gm., August 8, 1962, MCT 2741; ♂, June 23, 1963, ADG 155; ♀, May 25, 1963, ADG 109. Tiger Estate: ♂, November 25, 1962, MCT 3324.

Next to the Brown Barbet, this was perhaps the most common barbet at the Cocoa Research Station and was often the only bird heard in the heat of the day. On three occasions birds were observed clinging to the side of a tree as a woodpecker might, pecking away at dead wood. This species was seen both in the cocoa and primary forest.

Megalaima mystacophanes mystacophanes (Temminck): Gaudy Barbet.—*Specimens,* 8: Cocoa Research Station: ♀, 60.3 gm., July 25, 1962; ♂ testis 8 × 5 mm., 79.2 gm., August 9, 1962, MCT 2749; ♂ testis 9 × 5 mm., September 1, 1962, MCT 2845; ♀, September 25, 1962, MCT 2950; ♀, April 30, 1963, ADG 88. 12 mi. N Kalabakan: ♂, October 20, 1962, MCT 3103. 5.5 mi. SW Tenom: ♂ testis 8 × 6 mm., December 25, 1962, MCT 3530; ♀, December 25, 1962, MCT 3537.

This common bird lived in the secondary and primary forest and cocoa. I saw it at all localities. At least two calls were given by this species. One was a simple *took* with a long pause between calls; the other was as described by Smythies (1960:323).

The birds fed from high in trees down to nearly ground level. This species like *M. chrysopogon,* clung to the sides of trees and pecked at dead wood.

Megalaima australis duvauceli (Lesson): Little Barbet.—*Specimens,* 3: Cocoa Research Station: ♂ testis 7 × 5 mm., 35.2 gm., August 1, 1962, MCT 2692; ♂ testis 9 × 5 mm., August 1, 1962, MCT 2699; ♀ ovary granular, 33.0 gm., August 1, 1962, MCT 2704.

I was unable to make detailed observations on this species. All specimens were taken from a high feeding tree, where it was impossible to identify them before hand.

Indicator archipelagicus Temminck: Malaysian Honey-guide.—*Specimens,* 2: Cocoa Research Station: ♀ ovary minute, 29 November 1962, MCT 3394. Tenom: ♂ testis 3 × 2 mm., January 5, 1963, MCT 3580.

The specimen from the Cocoa Research Station was taken in a net in the cocoa and the Tenom bird was taken in a net in the middle of Tenom, both in garden areas. These two specimens differ in coloration from Bornean birds in the U. S. National Museum; I think the difference results from "foxing" of the older specimens. Specimens have been taken previously in North Borneo on the Bengkoka River, Lumbidan, and on the Mengalong River (Smythies, 1957:669). Mary Norman saw this honey-guide once at the Quoin Estate in 1962 (Smythies, 1963:279).

Sasia abnormis (Temminck): Rufous Piculet.—*Specimens,* 13: Cocoa Research Station: ♂ testis 3 × 2 mm., molting, July 10, 1962, MCT 2612; ♀, September 24, 1962, MCT 2940; ♀, December 1, 1962, MCT 3411; ♂, July 9, 1963, ADG 177; ♂, July 7, 1963, ADG 166; ♂, June 14, 1963, ADG 135. 12 mi. N Kalabakan: ♀, October 17, 1962, MCT 3061. 5.5 mi. SW Tenom: ♂, December 19, 1962, MCT 3470; ♀, December 23, 1962, MCT 3517; ♂, December 24, 1962, MCT 3529; ♀, December 27, 1962, MCT 3541. Oil Palm Research Station: ♀, August 24, 1963, ADG 257; ♂, August 15, 1963, ADG 242.

The piculet was common in the secondary undergrowth near the Cocoa Research Station, and was taken once in the primary forest. One bird was seen sitting on a small branch about 10 feet up at a right angle to the branch. It did not ascend the tree like a woodpecker. This species was also taken in the moss forest near Tenom.

Picus puniceus observandus (Hartert): Crimson-winged Woodpecker.—*Specimens,* 2: Cocoa Research Station: ♀, 65.8 gm., July 27, 1962, MCT 2671; ♂, September 27, 1962, MCT 2973.

This woodpecker was observed twice, both times in primary forest at the Cocoa Research Station.

Picus mentalis humei (Hargitt): Checkered-throated Woodpecker.—

Specimens, 2: Cocoa Research Station: ♀, 93.3 gm., July 23, 1962, MCT 2642; sex?, 107.0 gm., August 5, 1962, MCT 2733.

I saw this bird only twice, in primary forest.

Picus miniaceus malaccensis Latham: Banded Red Woodpecker.—*Specimen,* 1: Cocoa Research Station: ♂ testis 8 × 5 mm., 79.5 gm., August 4, 1962, MCT 2722.

On August 4 I saw two birds of this species together in badly disturbed primary forest and took the specimen listed above.

Micropternus brachyurus badiosus (Bonaparte): Rufous Woodpecker.—*Specimens,* 5: Cocoa Research Station: ♀ brood patch, 4 to 5 old collapsed follicles, 73.2 gm., July 3, 1962, MCT 2584; ♀, 65.4 gm., July 25, 1962, MCT 2658; ♂ testis 2 × 1 mm., 66.7 gm., July 25, 1962, MCT 2659. Tiger Estate: ♂, June 23, 1963, ADG 158; ♀, June 23, 1963, ADG 159.

I saw this woodpecker but twice, both times at the Cocoa Research Station. A female taken from a dead tree in the cocoa may have been just finishing nesting activities, judging from the size of the ova. A pair seen feeding on the ground near a brush pile in secondary forest was collected. The stomachs contained ants.

Dendrocopos canicapillus aurantiiventris (Salvadori): Oriental Pygmy Woodpecker.—*Specimens,* 2: Cocoa Research Station: sex?, July 22, 1962, MCT 2635; ♂ testis 3 × 2 mm., 23.5 gm., molting, August 25, 1962, MCT 2807.

On July 22 four individuals were feeding on dead trees in the cocoa. They made a *cheep cheep* sound, rattling calls, and drummed. On August 25, 1962, two were feeding in dead trees in the cocoa. The testes of specimen MCT 2807 were probably regressing since it was beginning the molt.

Meiglyptes tristis micropternus Hesse: Fulvous-rumped Barred Woodpecker.—*Specimens,* 2: Cocoa Research Station: ♀, 31.7 gm., July 7, 1962, MCT 2607; ♂, May 28, 1963, ADG 115.

Compared with *M. tukki,* this species was comparatively rare. I saw two on July 7 working in a living tree some 15 feet above the ground. The tree was only 20 feet high and had dense foliage. The birds gave a rattling call note of about two seconds duration; it sounded like a typical woodpecker call. The single call note can be rendered *cheet.* They were also heard drumming, but only softly. The stomachs contained ants, which probably are what the two woodpeckers were feeding on in the green tree.

Meiglyptes tukki tukki (Lesson): Buff-necked Barred Woodpecker.—*Specimens,* 13: Cocoa Research Station: ♂ testis 2 × 1 mm., heavy molt, July 10, 1962, MCT 2614; ♀, 53.3 gm., July 28, 1962, MCT 2677; ♂, 51.5 gm., July 28, 1962, MCT 2679; ♀, 48.7 gm., July 28, 1962, MCT 2678; ♂, December 2, 1962, MCT 3423; ♀, December 2, 1962, MCT 3424; ♀, December 2, 1962, MCT 3425. 12 mi. N Kalabakan: ♀, October 26, 1962, MCT 3153. Telipok: ♀, March 24, 1962, ADG 37. Agriculture Oil Palm Research Station: ♀, October 4, 1963, ADG 292; ♀, August 15, 1963, ADG 238; ♀, August 14, 1963, ADG 234. Pintasan Agriculture Station: ♀, October 17, 1963, ADG 313.

This was the most common woodpecker at the Cocoa Research Station. A flock of four was seen on July 28, 1962, and on December 2, 1962, I took three simultaneously in one mist net. The species has flocking tendencies. Calls heard were a typical woodpecker rattle.

Dinopium rafflesi dulitense Delacour: Olive-backed Three-toed Woodpecker.—*Specimens,* 4: Cocoa Research Station: ♂ testis 11 × 7 mm., July 12, 1962, MCT 2620; ♂, September 6, 1962, MCT 2879. 12 mi. N Kalabakan: ♂, October 20, 1962, MCT 3097. Oil Palm Research Station: ♂, August 12, 1963, ADG 227.

The species was taken in both primary and secondary forest. The specimen collected at the Cocoa Research Station on July 12 suggests that the species breeds there.

Dryocopus javensis javensis (Horsfield): Great Black Woodpecker.—*Specimens,* 4: Cocoa Research Station: ♀ old brood patch, 284.7 gm., light body and tail molt, July 6, 1962, MCT 2601; ♂ by plumage, July 19, 1962, MCT 2625; ♀, June 25, 1963, ADG 162; ♂, May 26, 1963, ADG 112.

This species was common at the Cocoa Research Station. On June 30, 1962, a flock of six was moving through secondary forest. On July 6, 1962, I saw four in dead trees in one of the cocoa fields.

Mulleripicus pulverulentus pulverulentus (Temminck): Great Slaty Woodpecker.—*Specimen,* 1: Tiger Estate: ♂, November 25, 1962, MCT 3326.

I saw this species once at the Cocoa Research Station, where a flock of four was feeding 30 feet up in secondary forest about 100 feet high on October 4, 1962.

Blythipicus rubiginosus parvus Chasen and Kloss: Maroon Woodpecker.—*Specimens,* 2: Cocoa Research Station: ♂, September 28, 1962, MCT 2975. 12 mi. N Kalabakan: ♂ imm., October 17, 1962, MCT 3062.

I saw this bird sporadically while I was on the east coast. It seemed to prefer secondary forest that had some undergrowth and was invariably flushed from the understory.

Chrysocolaptes validus xanthopygius Finsch: Orange-backed Woodpecker.—*Specimens,* 4: Cocoa Research Station: ♂, light body and wing molt, July 2, 1962, MCT 2575; ♂ testis 5 × 3 mm., 168.5 gm., July 23, 1962, MCT 2640; ♀, 176.1 gm., July 23, 1962, MCT 2641; ♂, September 28, 1962, MCT 2976.

This was one of the more common woodpeckers at the Cocoa Research Station. I saw it throughout the period I was there, in secondary forest and dead trees in the cocoa fields.

Calyptomena viridis gloriosa Deignan: Green Broadbill.—*Specimens,* 10: Cocoa Research Station: ♀, 67.4 gm., August 1, 1962, MCT 2698; ♀, 53.2 gm., September 16, 1962, MCT 2927; ♀, May 6, 1963, ADG 106; ♂, June 18, 1963, ADG 148; ♀ by plumage, June 26, 1963, ADG 164. 12 mi. N Kalabakan: ♀, October 12, 1962, MCT 3015; ♀, October 20, 1962, MCT 3098; ♂, October 22, 1962, MCT 3122. Oil Palm Research Station: ♀, August 15, 1963, ADG 240. Pintasan: ♂, October 16, 1963, ADG 310.

Sight records of this species are evidently a poor indication of its abundance, because I saw but one in the field at the Cocoa Research Station, a male sitting in the top of cocoa tree about eight feet up. All the specimens were netted, and the number so taken indicates not only that the species is common but also that it frequents the lower levels of the forest as well as the tops of tall trees (as noted by Smythies, 1960:339).

Cymbirhynchus macrorhynchus macrorhynchus (Gmelin): Black-and-Red Broadbill.—*Specimens,* 2: Kalabakan: ♂, November 16, 1962, MCT 3296. Tiger Estate: ♂, November 25, 1962, MCT 3321.

This species was seen only at Kalabakan, where I caught two in one net in dense secondary forest.

Eurylaimus ochromalus ochromalus Raffles: Black-and-Yellow Broadbill.—*Specimens,* 9: Cocoa Research Station: ♂, 32.0 gm., July 28, 1962, MCT 2682; ♂, 32.0 gm., August 1, 1962, MCT 2747; ♂, 33.8 gm., August 10, 1962, MCT 2753; ♀, 34.0 gm., September 11, 1962, MCT 2892; ♂, 34.7 gm., September 14, 1962, MCT 2926; ♀, September 26, 1962, MCT 2968; ♂, April 27, 1963, ADG 71. Agricultural Station Gum-Gum: ♀, September 26, 1963, ADG 284. Pintasan Agriculture Station: ♀, October 16, 1963, ADG 311.

This broadbill was common at the Cocoa Research Station in cocoa fields and adjacent secondary forest; it was never seen in primary forest. On September 4, 1962, I saw 10 to 15 in the cocoa, moving in a loose flock. The birds uttered call notes and at the same time bowed their heads sharply, as if to emphasize the call. Frequent supplanting, attacks, and other aggressive interactions were seen. The species was heard and observed also at a place 12 miles north of Kalabakan, at the edge of, but never in, primary forest.

Eurylaimus javanicus brookei Robinson and Kloss: Banded Broadbill.—*Specimen,* 1: Cocoa Research Station: ♂ testis 7 × 4 mm., 81.8 gm., July 25, 1962, MCT 2660.

This broadbill was seen only on two occasions at the Cocoa Research Station, both times at the edge of the primary forest.

Pitta baudi Muller and Schlegel: Blue-headed Pitta.—*Specimens,* 6: 12 mi. N Kalabakan: ♀, October 17, 1962, MCT 3067; ♀, October 23, 1962, MCT 3131; ♂, October 30, 1962, MCT 3182; ♀, October 30, 1962, MCT 3185; ♀, November 5, 1962, MCT 3212; ♂ testis 4 × 3 mm., November 6, 1962, MCT 3213.

The Blue-headed Pitta was abundant at the Kalabakan collecting locality, in primary forest. It was seen only once at the Cocoa Research Station.

The voice of this bird was a one-note whistle with a terminal inflection. It reminded me of a small child crying. When one called, it was usually in chorus with several others.

Pitta guajana schwaneri Bonaparte: Banded Pitta.—*Specimens,* 4: Cocoa Research Station: ♀ imm., 63.4 gm., July 24, 1962, MCT 2651; ♂ testis 6 × 3 mm., 81.5 gm., August 4, 1962, MCT 2723; ♀ imm., 71.8 gm., August 4, 1962, MCT 2724; ♂, June 15, 1963, ADG 145.

The specimens were taken in primary forest. This pitta was exceedingly tame, often moving along only 20 feet ahead of the observer. The one adult male taken hopped along the forest floor, occasionally jumping up on a log or plant to look back. It finally flushed and flew about 30 feet ahead of me to a log; there it gave a call which can be rendered as *shewo,* repeated at 10- to 15-second intervals. The call was much like that of *Pitta sordida.*

Pitta brachyura moluccensis (P. L. S. Müller): Blue-winged Pitta.—*Specimen,* 1: Tenom: ♀ oviduct slightly enlarged, edematized brood patch, December 31, 1962, MCT 3544.

The specimen was taken in a net stretched across a dry stream near the Padas River in a relatively open area near a coconut grove with some bamboo and elephant ears nearby.

Pitta sordida mulleri Bonaparte: Green-breasted Pitta.—*Specimens,* 2:

Cocoa Research Station: ♀, May 1, 1963, ADG 96; ♀, July 15, 1963, ADG 203.

The discovery of this bird by Garcia was a surprise. I was familiar with its habits and calls in the Philippines, and in four months I never heard or observed it at the Cocoa Research Station. Perhaps the specimens were migrants.

Hirundo tahitica abbotti Oberholser: Pacific Swallow.—*Specimen,* 1: Cocoa Research Station: ♂, April 26, 1963, ADG 58.

This species was common at most localities on the east coast. On June 25, 1962, a pair was building a nest under the Cocoa Research Station laboratory. On July 21 young were observed leaving the nest, at the research station rest house.

Hirundo rustica gutturalis Scopoli: Common Swallow.—*Specimens,* 9: 12 mi. N Kalabakan: ♂, November 10, 1962, MCT 3238; ♂, November 10, 1962, MCT 3239; ♀, November 12, 1962, MCT 3257; ♀, November 12, 1962, MCT 3258; ♂, November 12, 1962, MCT 3259; ♀, November 12, 1962, MCT 3260; ♂, November 13, 1962, MCT 3268; ♀, November 13, 1962, MCT 3269; ♀, November 13, 1962, MCT 3270.

I saw this migrant at Semporna on August 19, 1962; soon it was the most common swallow at each of the localities where seen.

Cecropsia striolata striolata Temminck and Schlegel: Striated Swallow.—While in Kalabakan on November 3, 1962, I saw a swallow that differed markedly from others in town. I could not see the breast, but the rump was conspicuously tawny, clearly indicating that the bird belonged to this species. There are but two specimens from Borneo, both from southwestern Sarawak (Smythies, 1960:353). D. M. Batchelor records the species from Kimanis Bay but gives no dates other than November-December (Smythies, 1963:280). Batchelor's observation and mine provide the first records for North Borneo.

Dicrurus aeneus malayensis (Blyth): Bronzed Drongo.—*Specimen,* 1: 12 mi. N Kalabakan: ♀, October 20, 1962, MCT 3104.

This drongo was seen only once, when a flock of three to five was feeding late one evening in a clearing where the trees had been cut down the day before.

Dicrurus paradiseus brachyphorus (Bonaparte): Large Racket-tailed Drongo.—*Specimens,* 5: Cocoa Research Station: ♀ immature, 58.2 gm., August 4, 1962, MCT 2727; ♀, 65.1 gm., August 20, 1962, MCT 2786; ♂, December 1, 1962, MCT 3413. 12 mi. N Kalabakan: ♀, October 20, 1962, MCT 3102. Kalabakan: ♂, November 18, 1962, MCT 3303.

I seldom saw this species in the cocoa at Quoin Hill. Twelve miles north of Kalabakan it was common in tree tops 150 feet up, foraging in the upper canopy.

Oriolus xanthonotus consobrinus Ramsay: Malaysian Black-headed Oriole.—*Specimens,* 9: Cocoa Research Station: ♂ imm., 41.8 gm., July 22, 1962, MCT 2639; ♀, 40.7 gm., July 23, 1962, MCT 2644; ♂ testis 1 × 1 mm., 48.2 gm., July 24, 1962, MCT 2653; ♀ imm., 36.3 gm., July 28, 1962, MCT 2681; ♂ imm., 40.4 gm., August 25, 1962, MCT 2804; ♂, September 26, 1962; MCT 2962; ♂, November 29, 1962, MCT 3381; ♀, December 2, 1962, MCT 3426. 12 mi. N Kalabakan: ♂, October 28, 1962, MCT 3180.

This oriole was common in the cocoa and in secondary forest surrounding the cocoa at Quoin Hill.

Platylophus galericulatus coronatus (Raffles): Crested Jay.—*Specimens,* 4: 12 mi. N Kalabakan: ♀, October 17, 1962, MCT 3068; ♀, October 21, 1962, MCT 3116; ♂, October 21, 1962, MCT 3117; ♂, October 21, 1962, MCT 3118.

This jay was observed several times at the forest camp at Kalabakan. The bird utters a metallic chattering noise much like that of other jays, except for the metallic quality. I observed it also in moss forest 5.5 miles north of Tenom.

Comparison of my specimens with series in the U. S. National Museum and the American Museum of Natural History indicates wide variation within this species in Borneo. The specimens vary considerably in depth of brown, some approaching *P. g. lemprieri* and others *P. g. coronatus.* Because of this wide variation I have not recognized the subspecies *lemprieri* and place all specimens from Borneo under *coronatus.*

Platysmurus leucopterus aterrimus (Temminck): Black Crested Magpie.—*Specimens,* 4: Cocoa Research Station: ♀ brood patch refeathering, 181.6 gm., July 21, 1962, MCT 2628; ♀ imm., 143.4 gm., July 21, 1962, MCT 2629; ♀, September 4, 1962, MCT 2865; ♂, 178.0 gm., September 6, 1962, MCT 2880.

The Black Crested Magpie was common at Quoin Hill in secondary forest and cocoa. At the Kalabakan forest camp, I saw a flock of 10 to 20 feeding 70 to 100 feet up in a tree in primary forest.

Corvus enca compilator Richmond: Slender-billed Crow.—*Specimen,* 1: Pintasan Agricultural Station: ♀, October 17, 1963, ADG 315.

Small flocks in the cocoa and secondary forest were common at the Cocoa Research Station.

Pityriasis gymnocephala (Temminck): Bald-headed Wood Shrike.—*Specimens,* 7: Cocoa Research Station: ♂ one testis, 115.0 gm., October 4, 1962, MCT 2987; ♀ largest ova 15 mm., well-developed brood patch, oviduct enlarged, 140.0 gm., October 4, 1962, MCT 2988; ♂ testis 8 × 5 mm., 121.0 gm., October 4, 1962, MCT 2989. 12 mi. N Kalabakan: ♂, November 8, 1962, MCT 3224; ♀, November 8, 1962, MCT 3225; ♂, November 8, 1962, MCT 3226; ♀, November 8, 1962, MCT 3227.

These birds first drew my attention at Quoin Hill by their peculiar whistle, which Smythies (1960:491) calls a "nasal whine." They seem not to descend lower than 30 feet above the ground. They are exceedingly tame; I shot at them two to four times without frightening them off. They were in badly disturbed primary forest at Quoin Hill. At a point 12 miles north of Kalabakan, I found them in primary forest. I took four birds from a flock of five or six. Later in the afternoon, I heard another group in the tops of trees 150 feet high. They seemed to be fairly common, judging by the frequency with which the calls were heard. One of the birds I shot was only wounded and set up such a clamor that soon the rest of the flock approached, seemingly in response to the distress calls. Some individuals came within 20 feet of me. The noise also attracted an accipiter.

Some of the specimens were made into skeletons, which I think show important indications of the systematic position of this species. The Bald-headed Wood Shrike has been placed in various families. Gadow (1883:90) placed it with the Cracticidae, with its closest relative being *Cracticus.* Ama-

don (1956) thought that it was best left in the Prionopidae, with subfamily status. Hachisuka (1953) concluded that its closest affinities were with *Cracticus* of the family Cracticidae. The latest reviser, A. L. Rand (*in* Peters *et al.*, 1960:364-365), places it in the Laniidae. A brief comparison of my skeletons of *Pityriasis* tended to confirm Gadow's and Hachisuka's conclusion that it belongs with the Cracticidae. I think that it is best placed in this family, with subfamily status (Pityriasinae).

Sitta frontalis corallipes (Sharpe): Velvet-fronted Nuthatch.—*Specimens,* 3: Cocoa Research Station: ♀ imm., 14.0 gm., July 23, 1962, MCT 2646; ♂ imm., 13.0 gm., August 20, 1963, MCT 2780; ♂ imm., August 27, 1962, MCT 2820.

I saw several nuthatches feeding in secondary forest at Quoin Hill and one 12 miles north of Kalabakan. One was observed feeding about 100 feet up in a dipterocarp.

Pellorneum capistratum morrelli Chasen and Kloss. Black-capped Jungle Babbler.—*Specimens,* 7: Cocoa Research Station: ♂ testis 3 × 2 mm., 21.1 gm., July 27, 1962, MCT 2667; ♀, 21.4 gm., July 31, 1962, MCT 2690; ♂, September 24, 1962, MCT 2938; ♀, June 13, 1963, ADG 131; ♀ imm., June 14, 1963, ADG 140; ♀, July 7, 1963, ADG 168. Ulu Balung Cocoa Estate: ♀, July 11, 1963, ADG 188.

This species was seen 12 miles north of Kalabakan and at Quoin Hill. It was fairly common and could be seen running on the ground ahead of the observer, occasionally hopping up on a brush pile or branch, seemingly to make a quick survey before moving back to the ground. It preferred primary forest but was occasionally observed in the primary-secondary forest edge vegetation.

Trichastoma pyrrhogenys canicapillum (Sharpe): Temminck Jungle Babbler.—*Specimens,* 13: 5.5 mi. SW Tenom: ♀, December 17, 1962, MCT 3445; ♂, December 17, 1962, MCT 3446; ♂, December 17, 1962, MCT 3452; ♂, December 18, 1962, MCT 34554; ♀ collapsed follicles, brood patch, December 18, 1962, MCT 3455; ♂, December 18, 1962, MCT 3460; ♂ testis 2 × 1 mm., December 18, 1962, MCT 3461; ♂, December 19, 1962, MCT 3474; ♂ testis 6 × 3 mm., December 19, 1962, MCT 3475; ♂, December 22, 1962, MCT 3505; ♂, December 24, 1962, MCT 3528; ♀ imm., December 25, 1962, MCT 3532; ♂ testis 5 × 3 mm., December 25, 1962, MCT 3533.

This species was common in the moss forest near Tenom. The female specimen with collapsed follicles indicates that some of the birds were in breeding condition. All specimens were netted.

Trichastoma malaccense poliogenys (Strickland): Short-tailed Jungle Babbler.—*Specimens,* 17: Cocoa Research Station: ♂ testis 7 × 4 mm., 24.5 gm., July 31, 1962, MCT 2687; ♀, September 5, 1962, MCT 2874; ♀, September 24, 1962, MCT 2941; ♂, November 29, 1962, MCT 3387; ♀, November 29, 1962, MCT 3388; ♂, December 1, 1962, MCT 3400; ♀, November 12, 1962, MCT 3262. Kalabakan: ♂, November 16, 1962, MCT 3292. Cocoa Research Station: ♂, June 11, 1963, ADG 123; ♂, June 12, 1963, ADG 127; ♀, June 13, 1963, ADG 132. Ulu Balung Cocoa Estate: ♂, July 9, 1963, ADG 179; ♂, July 9, 1963, ADG 179 (*sic*). Oil Palm Research Station: ♂, August 10, 1963, ADG 219; ♂, August 12, 1963, ADG 225; ♀, August 13, 1963, ADG 236; ♀, August 23, 1963, ADG 255.

This terrestrial species was common in primary forest, and occasionally in secondary forest, in low trees or around brush piles. On September 24, by "squeaking," I so aroused one bird that it ran back and forth on a limb of a

fallen tree in great agitation. The specimen taken on November 12 was in heavy molt; it lacked tail feathers and the primaries were being replaced.

Trichastoma bicolor (Lesson): Ferruginous Jungle Babbler.—*Specimens,* 6: 12 mi. N Kalabakan: ♂, October 24, 1962, MCT 3143; ♀, October 26, 1962, MCT 3161; ♂, November 10, 1962, MCT 3135; ♀, November 12, 1962, MCT 3255. Oil Palm Research Station: ♂, August 12, 1963, ADG 266; ♀, August 28, 1963, ADG 269.

All specimens were taken in primary forest.

Trichastoma sepiarium harteri (Chasen and Kloss): Horsfield Jungle Babbler.—*Specimens,* 6: Cocoa Research Station: ♂ testis 8 × 5 mm., 25.7 gm., July 24, 1962, MCT 2652; ♂ testis 8 × 5 mm., 28.2 gm., July 27, 1962, MCT 2668; ♂ testis 8 × 7 mm., 28.2 gm., July 31, 1962, MCT 2688; ♂, June 15, 1963, ADG 142. 12 mi. N Kalabakan: ♂ testis 8 × 5 mm., November 8, 1962, MCT 3233. Oil Palm Research Station: ♀, September 5, 1963, ADG 275.

This babbler tends to inhabit secondary growth more than does *T. malaccense* and was partly arboreal, occasionally ranging as high as 20 feet above ground. It occurred occasionally in flocks of four or five.

Malacopteron magnum magnum Eyton: Greater Red-headed Babbler.—*Specimens,* 12: Cocoa Research Station: ♂ testis 7 × 5 mm., September 7, 1962, MCT 2886; ♂ testis 9 × 5 mm., October 4, 1962, MCT 2990; ♂, November 30, 1962, MCT 3437; ♀, November 27, 1962, MCT 3340; ♀, April 30, 1963, ADG 91; ♂, June 14, 1963, ADG 136; ♂, July 9, 1963, ADG 178. Ulu Balung Cocoa Estate: ♂, July 11, 1963, ADG 191; ♂, July 16, 1963, ADG 205. 12 mi. N Kalabakan: ♂, October 22, 1962, MCT 3124; ♀, October 28, 1962, MCT 3176; ♂, October 28, 1962, MCT 3177.

This babbler was common at the Cocoa Research Station but uncommon elsewhere. It seemed to prefer primary forest and was only rarely seen in the cocoa. My series shows that this species was common at Quoin Hill and *M. cinereum* was rare, while the opposite obtained 12 miles north of Kalabakan. For the moment this cannot be explained. Possibly these two species are competitive and tend toward mutual exclusion. Since the birds were mostly netted, it is assumed that I obtained a random sample. My observations at Quoin Hill seem to bear out the specimen record.

The specimens in my series of *M. m. magnum* are more nearly black on the crown than those labelled *M. m. saba* in the U. S. National Museum (from the Segah River), but there was much variation in the amount of black on the crown in all series examined. I consider *M. m. saba* to be synonymous with *M. m. magnum.*

Malacopteron cinereum cinereum Eyton: Lesser Red-headed Babbler.—*Specimens,* 29: Cocoa Research Station: ♂, December 2, 1962, MCT 3428; ♀, June 11, 1963, ADG 124; ♂, July 9, 1963, ADG 178. 12 mi. N Kalabakan: ♂, October 13, 1962, MCT 3025; ♀, October 13, 1962, MCT 3030; ♂, October 13, 1962, MCT 3032; ♀, October 14, 1962, MCT 3042; ♂, October 14, 1962, MCT 3043; ♀, October 16, 1962, MCT 3059; ♂, October 21, 1962, MCT 3119; ♂, October 22, 1962, MCT 3128; ♀, October 24, 1962, MCT 3136; ♂, October 28, 1962, MCT 3178; sex?, October 31, 1962, MCT 3188; ♀, November 7, 1962, MCT 3219; ♀, November 7, 1962, MCT 3220; ♂, November 12, 1962, MCT 3263; ♀, November 12, 1962, MCT 3264. Kalabakan: ♂, November 15, 1962, MCT 3282; ♂, November 15, 1962, MCT 3284; ♀, November 15, 1962, MCT 3285. Ulu Balung Cocoa Estate: ♂, July 13, 1963, ADG 197. Oil Palm Research Station: sex?, August 16, 1963, ADG 245; ♀, August 28, 1963, ADG 272. Pintasan Agriculture Station: ♂, October 17, 1963, ADG 318; ♂, October 18, 1963, ADG 319; ♂, October

18, 1963, ADG 320; ♀, October 18, 1963, ADG 321; ♀, October 18, 1963, ADG 322. See remarks under *M. magnum*.

Malacopteron magnirostre cinereocapillum (Salvadori): Brown-headed Babbler.—*Specimens*, 20: Cocoa Research Station: ♂ testis 5 × 3 mm., 20.4 gm., July 23, 1962, MCT 2647; ♂ testis 2 × 1 mm., 20.0 gm., July 24, 1962, MCT 2656; ♂ testis 1 × 1 mm., 20.5 gm., July 24, 1962, MCT 2657; ♂, 20.4 gm., July 27, 1962, MCT 2669. 12 mi. N Kalabakan: ♂, October 10, 1962, MCT 2994; ♂ testis 5 × 3 mm., October 12, 1962, MCT 3016; ♀, October 12, 1962, MCT 3017; ♂, October 13, 1962, MCT 3026; ♀, October 13, 1962, MCT 3028; ♂, October 17, 1962, MCT 3070; ♂, October 19, 1962, MCT 3083; ♂, October 19, 1962, MCT 3084; ♂ testis 5 × 4 mm., October 20, 1962, MCT 3108; ♂, October 26, 1962, MCT 3158; ♀, October 26, 1962, MCT 3159; ♂, November 11, 1962, MCT 3253; ♀, November 11, 1962, MCT 3254. 5.5 mi. SW Tenom: ♂, December 19, 1962, MCT 3462. Oil Palm Research Station: ♀, August 28, 1963, ADG 265.

This babbler inhabits the understory of primary forest, and occasionally is seen in secondary forest scrub. A specimen was taken at 4,000 feet elevation in moss forest near Tenom. The breeding season is seemingly in June and July but there is indication of gonadal activity in males in October (MCT 3108). On October 15, 1962, I observed an individual feeding on the rough bark of a large dipterocarp. The bird was clinging to the bark much as a nuthatch would, hopping along the vertical trunk upside down, laterally and straight up. Other birds of the species were feeding close by in small trees about 20 feet tall.

Pomatorhinus montanus borneensis Cabanis: Chestnut-backed Scimitar Babbler.—*Specimens*, 3: Cocoa Research Station: ♂ testis 5 × 2 mm., 33.1 gm., July 23, 1962, MCT 2643; ♂ testis 2 × 1 mm., 28.2 gm., July 24, 1962, MCT 2655. 5.5 mi. SW Tenom: ♂, December 22, 1962, MCT 3496.

This bird of the understory in primary forest was seen in only one other situation, 12 miles north of Kalabakan it was feeding in a clearing near our camp.

Ptilocichla leucogrammica (Bonaparte): Bornean Wren-babbler.—*Specimens*, 3: Ulu Balung Cocoa Estate: ♂, July 17, 1963, ADG 207: ♀ one egg in oviduct, July 19, 1963, ADG 211. Oil Palm Research Station: ♀ egg in oviduct, August 13, 1963, ADG 230.

Garcia netted three specimens in primary forest. This bird is known from Borneo only from a few specimens (Smythies, 1960:410). In North Borneo, it has been known previously only from Bettotan on the east coast (Smythies, 1960:410). The additional records published herewith also are for the east coast.

Kenopia striata (Blyth): Striped Wren-babbler.—*Specimens*, 11: Cocoa Research Station: ♀, 21.1 gm., July 24, 1962, MCT 2649; ♂ testis 4 × 3 mm., 19.6 gm., July 24, 1962, MCT 2640; ♂ testis 2 × 1 mm., 18.7 gm., July 27, 1962, MCT 2670. 12 mi. N Kalabakan: ♀, October 28, 1962, MCT 3172; ♂, October 21, 1962, MCT 3114; ♀, October 22, 1962, MCT 3123; ♂, October 26, 1962, MCT 3157; ♂, October 30, 1962, MCT 3187; ♂, November 1, 1962, MCT 3192. Ulu Balung Cocoa Estate: ♂, July 21, 1963, ADG 213. Oil Palm Research Station: ♂, August 13, 1963, ADG 229; ♀, August 19, 1963, ADG 250.

This bird of primary forest is found occasionally in adjacent secondary forest and spends about three-fourths of its time running about on the ground, only occasionally ascending to the lower branches of trees. The song may be rendered as *kittle jank*, the first note being trilled and a bit higher than

the last, which is short and chopped off. This babbler appears to sing as it moves along the forest floor without stopping. It was observed foraging under leaves, and was common both at Quoin Hill and 12 miles north of Kalabakan, in groups of two or three birds.

Macronous gularis (Horsfield): Striped Tit-babbler.—I saw this bird at the Semporna Rest House feeding in shrubbery. It was not seen elsewhere.

Macronous ptilosus reclusus Hartert: Fluffy-backed Tit-babbler.—*Specimens,* 2: Kalabakan: ♂, November 15, 1962, MCT 3283. Oil Palm Research Station: sex?, August 23, 1963, ADG 254.

This bird was seen only at Kalabakan, in dense secondary growth. My specimen was in heavy molt.

Stachyris nigriceps hartleyi Chasen: Gray-throated Tree Babbler.—*Specimens,* 16: 5.5 mi. SW Tenom: ♂, December 17, 1962, MCT 3451; ♀, December 18, 1962, MCT 3456; ♂ testis 7 × 5 mm., December 18, 1962, MCT 3457; ♂ testis 6 × 3 mm., December 18, 1962, MCT 3458; ♀, December 18, 1962, MCT 3459; ♀ old brood patch, December 19, 1962, MCT 3471; ♂ testis 9 × 5 mm., December 19, 1962, MCT 3472; ♀ several collapsed follicles, December 19, 1962, MCT 3473; ♂ testis 6 × 4 mm., December 20, 1962, MCT 3480; ♂ testis enlarged, December 20, 1962, MCT 3481; ♀ imm., December 20, 1962, MCT 3482; ♂ testis 7 × 5 mm., December 20, 1962, MCT 3486; ♀, December 21, 1962, MCT 3493; ♂ testis 7 × 5 mm., December 21, 1962, MCT 3494; ♀ imm., December 21, 1962, MCT 3495; ♀ imm., December 22, 1962, MCT 3506.

This babbler was abundant in the moss forest above Tenom and appeared to be at the height of its breeding season in December.

The specimens were compared with material at the American Museum of Natural History and proved to be *S. n. hartleyi,* which has not previously been reported from North Borneo.

Stachyris poliocephala (Temminck): Gray-headed Tree Babbler.—*Specimens,* 8: Cocoa Research Station: ♂ testis 3 × 2 mm., 24.0 gm., July 28, 1962, MCT 2674; ♂, December 1, 1962, MCT 3414; ♀, December 1, 1962, MCT 3415. 12 mi. N Kalabakan: ♀, October 18, 1962, MCT 3072; sex?, October 29, 1962, MCT 3181; ♀, November 2, 1962, MCT 3202. Oil Palm Research Station: ♂, August 16, 1963, ADG 248; ♀, August 15, 1962, ADG 239.

This species of the secondary forest usually was associated with piles of brush or heavy growth of fern. I never saw it higher than three feet above the ground.

Stachyris nigricollis (Temminck): Black-necked Tree Babbler.—*Specimens,* 4: Cocoa Research Station: ♂, June 15, 1963, ADG 144. Ulu Balung Cocoa Estate: ♀, July 15, 1963, ADG 201. Oil Palm Research Station: ♂, August 12, 1963, ADG 224; ♀, August 19, 1963, ADG 251.

Although I worked in the same area and at the same time of year as did Garcia, I did not see this species.

Stachyris leucotis obscurata Mayr: White-necked Tree Babbler.—*Specimen,* 1: Oil Palm Research Station: ♂, September 5, 1963, ADG 274.

Garcia's specimen was taken in primary forest. Smythies (1960:418) states that most records come from sub-montane localities, except for those from Bettotan; the specimen is from an altitude of 40 feet, near Bettotan.

Stachyris maculata maculata (Temminck): Red-rumped Tree Babbler.—*Specimens,* 12: Cocoa Research Station: ♀ largest ova 2 mm., brood patch, July 10, 1962, MCT 2613; ♂, 25.8 gm., August 5, 1962, MCT 2731; ♂,

28.0 gm., August 5, 1962, MCT 2732. 12 mi. N Kalabakan: ♂ testis 3 × 3 mm., October 12, 1962, MCT 3006; ♀, October 12, 1962, MCT 3007; ♀, October 12, 1962, MCT 3008; ♂, October 12, 1962, MCT 3009. Cocoa Research Station: ♀, June 11, 1963, ADG 121; ♀, June 13, 1963, ADG 133; ♂, June 14, 1963, ADG 134. Oil Palm Research Station: ♀, August 14, 1963, ADG 235; ♀, August 15, 1963, ADG 237.

This babbler was common in small groups at Quoin Hill. Whitehead (1893:227) states that the species "frequents the true forest near the ground." I observed these babblers only in sub-canopy trees, at least 30 feet above the ground. Smythies (1960:419) stated that he had never seen this species in the forest undergrowth.

Stachyris erythroptera bicolor (Blyth): Red-winged Tree Babbler.—*Specimens,* 11: Cocoa Research Station: ♂ testis 2 × 1 mm., 13.4 gm., July 24, 1962, MCT 2654; ♀ imm., 13.0 gm., August 28, 1962, MCT 2832; ♀, 12.5 gm., August 28, 1962, MCT 2833; ♂, December 2, 1962, MCT 3432; ♀, December 2, 1962, MCT 3433. 12 mi. N Kalabakan: ♂, October 10, 1962, MCT 2995; ♂, November 6, 1962, MCT 3215; ♂, November 7, 1962, MCT 3218. 5.5 mi. SW Tenom: ♂ testis 3 × 1 mm., December 18, 1962, MCT 3463. Ulu Balung Cocoa Estate: ♂, July 10, 1963, ADG 184; ♂, July 17, 1963, ADG 206.

This species was seen most often in primary forest undergrowth, but occasionally as high as 10 feet up in small trees. I saw it also in and around brush piles in secondary forest. The one specimen from 5.5 mi. SW Tenom was taken in the moss forest. MCT 2833 was in heavy molt on the wings, head, and body.

Stachyris rufifrons sarawacensis Chasen: Hume's Tree Babbler.—*Specimen,* 1: Cocoa Research Station: ♂ testis 4 × 3 mm., November 28, 1962, MCT 3358.

There was no comparative material in the U. S. National Museum where I studied the specimen but it fits Chasen's original description of *S. r. sarawacensis.* H. G. Deignan (*in* Peters *et al.,* 1964:303) considered this subspecies doubtfully distinct from *S. r. poliogaster.*

The specimen was taken at a height of one and one-half feet in a mist net set along a path. The bird was caught when it attempted to cross the path from a patch of heavy undergrowth to a patch on the other side. Mary Norman observed them at Kalabakan (Smythies, 1963:281) in saplings. They should probably be considered birds of the understory.

Alcippe brunneicauda (Salvadori): Brown Quaker Babbler.—*Specimens,* 22: Cocoa Research Station: ♂ imm., 14.4 gm., August 20, 1962, MCT 2781; ♀, 14.9 gm., September 6, 1962, MCT 2877; ♀, September 25, 1962, MCT 2957; ♀, November 28, 1962, MCT 3361; ♀, November 28, 1962, MCT 3362; ♂, November 28, 1962, MCT 3376; ♂, November 28, 1962, MCT 3378; ♂ testis 5 × 3 mm., December 1, 1962, MCT 3410; ♂, December 2, 1962, MCT 3435; ♂, November 30, 1962, MCT 3440; ♂, November 30, 1962, MCT 3441. 12 mi. N Kalabakan: sex?, November 1, 1962, MCT 3194; ♂, November 11, 1962, MCT 3243; ♂, November 11, 1962, MCT 3245; ♂, November 11, 1962, MCT 3247; ♂, November 11, 1962, MCT 3248; ♂, November 12, 1962, MCT 3261; ♀, November 13, 1962, MCT 3267; ♀, November 10, 1962, MCT 3306. 5.5 mi. SW Tenom: ♀, December 22, 1962, MCT 3501; ♀, December 22, 1962, MCT 3502; ♀, December 22, 1962, MCT 3503.

Birds of this species were common in primary forest at the three localities listed under "specimens." They travel in small, loose flocks, calling as they move through the forest. Periodic calling, interspersed with periods of silence,

was characteristic of the species; vocalization of this sort may function in maintaining the unity of the well spaced flock.

Yuhina castaniceps everetti (Sharpe): Chestnut-headed Yuhina.—*Specimens,* 14: 5.5 mi. SW Tenom: ♀, December 19, 1962, MCT 3468; ♂ testis 6 × 3 mm., December 23, 1962, MCT 3512; ♂ testis 7 × 3 mm., December 23, 1962, MCT 3513; ♂ testis 6 × 3 mm., December 24, 1962, MCT 3520; ♀, December 24, 1962, MCT 3521; ♂ testis 5 × 3 mm., December 24, 1962, MCT 3523; ♂ testis 6 × 3 mm., December 24, 1962, MCT 3524; ♀, December 24, 1962, MCT 3525; ♀, December 24, 1962, MCT 3526; ♂ testis 6 × 3 mm., December 24, 1962, MCT 3527; ♂ testis 6 × 3 mm., December 28, 1962, MCT 3542; ♂ testis 6 × 3 mm., December 28, 1962, MCT 3543.

I saw several flocks of this species in moss forest at a point 5.5 miles southwest of Tenom. Some were observed going into cavities in the moss, where they apparently caught insects. They sometimes did this simultaneously, in several places on the same tree.

Yuhina zantholeuca brunnescens (Sharpe): White-bellied Yuhina.—*Specimens,* 4: 12 mi. N Kalabakan: ♀, October 12, 1962, MCT 3010; sex?, November 1, 1962, MCT 3193; sex?, December 22, 1962, MCT 3500; ♂ testis 7 × 4 mm., December 23, 1962, MCT 3519.

One flock of about five of these yuhinas was seen in primary forest at Kalabakan. Another small group was observed in the moss forest near Tenom.

Tephrodornis gularis frenatus Büttikofer: Hook-billed Graybird.—*Specimens,* 3: Cocoa Research Station: ♂, September 25, 1962, wing molt, MCT 2946; ♀, September 25, 1962, wing molt, MCT 2947; ♀, September 25, 1962, MCT 2948.

I observed this species twice in six months on the east coast. The three collected at the research station in the cocoa were in a family group. On November 9, 1962, I saw three birds feeding at the edge of the primary forest.

Coracina striata sumatrensis (S. Müller): Barred Graybird.—*Specimens,* 2: Tiger Estate: ♀, December 30, 1962; ♂, December 30, 1962.

Coracina fimbriata schierbrandi (Pelzeln): Lesser Graybird.—*Specimens,* 6: Cocoa Research Station: ♂ imm., 25.7 gm., July 22, 1962, MCT 2637; sex?, 29.5 gm., July 28, 1962, MCT 2676; ♂, 28.4 gm., August 5, 1962, MCT 2729; ♀, 30.0 gm., September 13, 1962, MCT 2917. 12 mi. N Kalabakan: ♀, October 25, 1962, MCT 3147. Tiger Estate: ♂, November 25, 1962, MCT 3317.

This species was common at the Cocoa Research Station, most common in the cocoa, and an occasional bird was observed in the primary forest.

The adult male (MCT 3317) from Tiger Estate was darker than any in the series of *C. f. schierbrandi* in The American Museum of Natural History, and closely approached a series *C. f. culminata* from Malaya in the same museum.

Hemipus hirundinaceus (Temminck): Black-winged Flycatcher Shrike.—*Specimen,* 1: Cocoa Research Station: ♀, 10.2 gm., July 21, 1962, MCT 2632.

The specimen was taken in the cocoa where it was sitting on a dead limb, occasionally darting out after insects, and provides the only record from this locality. At the collecting site 12 miles north of Kalabakan, however, it was seen several times feeding in small flocks in a clearing near a trail.

Hemipus picatus intermedius Salvadori: Bar-winged Flycatcher Shrike.—*Specimens,* 6: Cocoa Research Station: ♀ imm., August 27, 1962, MCT 2815; ♂ imm., August 27, 1962, MCT 2816; ♀, August 27, 1962, MCT 2817; ♀,

9.8 gm., September 12, 1962, MCT 2906; ♀, 10.2 gm., September 12, 1962, MCT 2907; ♂ imm., 8.7 gm., September 12, 1962, MCT 2908.

Smythies (1960:362) lists this species as a montane resident. However, the elevation of the Cocoa Research Station is only 750 feet, which is clearly submontane (Smythies, 1960:693). I saw the birds in a flock of three or four, feeding in shade trees in the cocoa fields. They acted like typical flycatchers, sitting on twigs and darting out after insects. On September 12, a flock of 10 was seen in the same area. Whitehead (1893:208) described the habits of the species as being like those of *Tephrodornis gularis* and not at all like those of a flycatcher.

Lalage nigra (Forster): Pied Triller.—Common in the lowlands near Tawau and Tuaran. On September 19, 1962, I saw an adult feeding one young on Siamil Island.

Pericrocotus igneus igneus Blyth: Fiery Minivet.—*Specimens,* 3: Cocoa Research Station: ♂, 15.8 gm., August 11, 1962, MCT 2764; ♂, 14.0 gm., August 11, 1962, MCT 2766; ♀, 15.2 gm., August 11, 1962, MCT 2767.

I saw this species only on August 11, 1962, when a flock of eight was seen feeding in a cocoa tree.

The female is somewhat darker than comparative material from Borneo, possibly owing to fresh plumage in my specimen and foxing in the older comparative material.

Pericrocotus flammeus insulanus Deignan: Scarlet Minivet.—*Specimens,* 5: Cocoa Research Station: ♂ testis 2 × 1 mm., 20.0 gm., July 7, 1962, MCT 2608; ♀, 19.7 gm., August 4, 1962, MCT 2728; ♂, 19.0 gm., August 23, 1962, MCT 2802. Tiger Estate: ♀, June 23, 1963, ADG 160; ♂, June 23, 1963, ADG 161.

This minivet was common at the Cocoa Research Station, where it usually inhabited the shade trees in the cocoa groves. The birds seen and the one taken on July 7 were all in heavy molt.

Pycnonotus eutilotus (Jardine and Selby): Crested Brown Bulbul.—*Specimens,* 2: Cocoa Research Station: ♀, December 2, 1962, MCT 3421; ♂, June 19, 1963, ADG 152.

The species was netted twice in much disturbed primary forest.

Pycnonotus melanoleucos (Eyton): Black and White Bulbul.—*Specimen,* 1: 12 mi. N Kalabakan: ♀, November 5, 1962, MCT 3211.

The specimen was caught in a mist net in primary forest. It was aberrant; the two outer tail feathers were white and it had a few white under tail coverts.

Pycnonotus squamatus borneensis Chasen: Scaly-breasted Bulbul.—*Specimens,* 2: Cocoa Research Station: ♀, 24.0 gm., August 2, 1962, MCT 2708; ♂ testis 4 × 3 mm., 22.2 gm., August 23, 1962, MCT 2802.

Both specimens were taken from a feeding tree, *Trema orientalis,* in which they were eating berries. This species of tree was used for shade in the cocoa.

Pycnonotus cyaniventris paroticalis (Sharpe): Gray-bellied Bulbul.—*Specimens,* 2: Cocoa Research Station: ♀ largest ovum 2 mm., 21.6 gm., August 25, 1962, MCT 2808; ♂ testis 7 × 4 mm., 20.5 gm., September 13, 1962, MCT 2916.

On August 23, 1962, I saw four in the cocoa but they took flight into the forest. I later collected two specimens from a shade tree, *Trema orientalis,* in which they were feeding upon the berries.

Pycnonotus atriceps atriceps (Temminck): Black-headed Bulbul.—*Specimens,* 9: Cocoa Research Station: ♀, April 29, 1963, ADG 85; ♀, April 27, 1963, ADG 72; ♀, April 20, 1963, ADG 90; ♂, April 27, 1963, ADG 69; ♂, April 28, 1963, ADG 79; ♂, April 26, 1963, ADG 61; ♂, April 28, 1963, ADG 81; ♂ juv., April 28, 1963, ADG 82; ♂, May 1, 1963, ADG 97.

I did not see this species in my stay at the Cocoa Research Station, and the specimens taken by Garcia constitute the only record. The juvenal plumage in one specimen indicates that the species breeds at Quoin Hill.

Pycnonotus zeylanicus (Gmelin): Yellow-crowned Bulbul.—It was common at Tuaran.

Pycnonotus goiavier gourdini Gray 1847: Yellow-vented Bulbul.—*Specimens,* 17: Tenom: ♀, December 31, 1962, MCT 3547; ♂ testis 9 × 6 mm., December 31, 1962, MCT 3548; ♀ oviduct regressing, old brood patch, December 31, 1962, MCT 3549; ♂, December 31, 1962, MCT 3550; ♀ oviduct nearly regressed, January 1, 1963, MCT 3556; ♀, January 1, 1963, MCT 3557; ♂ testis 9 × 7 mm., December 31, 1963, MCT 3558; ♂ testis enlarged, January 1, 1963, MCT 3559; ♀, January 1, 1963, MCT 3560; ♂, January 2, 1963, MCT 3562; ♀, January 2, 1963, MCT 3566; ♂, January 2, 1963, MCT 3567; ♂ testis 9 × 7 mm., January 2, 1963, MCT 3568; ♂, January 2, 1963, MCT 3569; ♀, January 2, 1963, MCT 3570; ♀, January 2, 1963, MCT 3571; ♂ testis 9 × 7 mm., January 2, 1963, MCT 3572.

Although this species was observed by me at the Cocoa Research Station, I was unable to obtain any specimens. It was also seen commonly at Semporna, Siamil Island, Kalabakan, Brantian Estate, and at Tuaran, always associated with cultivated areas. The birds obviously were breeding at Tenom in December, and several young were taken. In some, the molt of the wings, body, and tail had begun.

Pycnonotus plumosus hutzi Stresemann: Large Olive Bulbul.—*Specimens,* 8: Tenom: ♀, December 31, 1962, MCT 3551; ♂ testis 6 × 5 mm., January 1, 1963, MCT 3553; ♂ testis small, January 1, 1963, MCT 3554; ♂ testis 6 × 4 mm., January 4, 1963, MCT 3577; ♂ testis 5 × 4 mm., January 4, 1963, MCT 3578. Mt. Rumas: ♂, March 6, 1963, ADG 16; ♀, March 6, 1963, ADG 17; sex?, March 6, 1963, ADG 15.

The specimens were netted in scrub-grassland at Tenom. The size of the testes of the Tenom specimens indicated that the birds were breeding.

Pycnonotus brunneus brunneus Blyth: Red-eyed Brown Bulbul.—*Specimens,* 17: Cocoa Research Station: ♂ imm., 32.6 gm., July 22, 1962, MCT 2638; ♂ testis minute, 37.3 gm., August 2, 1962, MCT 2709; ♂ testis minute, 36.0 gm., August 3, 1962, MCT 2720; ♀ ovary granular, September 4, 1962, MCT 2867; ♂ testis 6 × 4 mm., September 4, 1962, MCT 2868; ♀ egg in oviduct, largest ovum 9 mm., 1 collapsed follicle, 30.0 gm., September 10, 1962, MCT 2894; ♂ testis small, September 25, 1962, MCT 2953; ♀, September 25, 1962, MCT 2954; ♂ testis small, November 27, 1962, MCT 3346; ♂ testis 4 × 2 mm., November 29, 1962, MCT 3380; ♂ testis small, November 29, 1962, MCT 3393; ♂ testis small, December 1, 1962, MCT 3402; ♂ testis small, December 1, 1962, MCT 3403; ♂ testis small, December 1, 1962, MCT 3404; ♀ ovary minute, December 1, 1962, MCT 3416; ♂ testis small, November 30, 1962, MCT 3438. Oil Palm Research Station: ♀, August 27, 1963, ADG 260.

This most common of the "brown" bulbuls at the Cocoa Research Station frequented shade trees (*Trema orientalis*). One bird fed on small red peppers, *Capsicum* sp. Some of the September-taken specimens were in breeding condition.

Pycnonotus simplex perplexus Chasen and Kloss: White-eyed Brown Bulbul.—*Specimens,* 3: 5.5 mi. SW Tenom: ♀ ovary granular, December 19,

1962, MCT 3469; ♂ testis 4 × 3 mm., December 20, 1962, MCT 3478; ♀ ovary granular, December 22, 1962, MCT 3499.

This bird was taken only in the moss forest at 4,000 feet elevation near Tenom. Smythies (1960:382) considered the species to be characteristic of the lowlands. Specimens were taken by Harrison in the Kelabit Uplands (Smythies, 1957:704) at 4,200 feet.

Pycnonotus erythrophthalmos salvadori (Sharpe): Lesser Olive-brown Bulbul.—*Specimens*, 15: Cocoa Research Station: ♂ testis 6 × 4 mm., 20.2 gm., August 12, 1962, MCT 2778; ♂ testis 6 × 5 mm., 19.8 gm., August 28, 1962, MCT 2830; ♀ ovary granular, 20.5 gm., August 28, 1962, MCT 2831; ♀ imm., 20.0 gm., September 14, 1962, MCT 2925; ♂ testis 7 × 5 mm., September 25, 1962, MCT 2928; ♂ ?, October 2, 1962, MCT 2983; ♀, November 27, 1962, MCT 3357; ♂ testis small, December 1, 1962, MCT 3405; ♂ testis minute, December 2, 1962, MCT 3420; ♂ testis small, December 1, 1962, MCT 3434; ♂ testis small, November 30, 1962, MCT 3439; ♀, April 26, 1962, ADG 63; ♂, July 7, 1963, ADG 170; ♂, July 7, 1963, ADG 171; ♂, July 8, 1963, ADG 176.

This species commonly fed in the shade trees (*Trema orientalis*), along with other species of bulbuls. I occasionally saw individuals in primary forest.

Criniger bres gutturalis (Bonaparte): Olive White-throated Bulbul.—*Specimens*, 25: Cocoa Research Station: ♀ ovary regressed, 41.4 gm., July 27, 1962, MCT 2666; ♀, 46.0 gm., July 28, 1962, MCT 2672; ♂, 51.2 gm., July 31, 1962, heavy molt, MCT 2685; ♂ testis 4 × 3 mm., 52.6 gm., August 2, 1962, MCT 2710; ♂, November 27, 1962, MCT 3353; ♀, November 27, 1962, MCT 3354; ♀, June 14, 1963, ADG 138; ♀, July 8, 1963, ADG 172; ♂, July 7, 1963, ADG 173; sex?, July 11, 1963, ADG 190. 12 mi. N Kalabakan: ♀, October 16, 1962, MCT 3052; ♂ testis small, October 22, 1962, MCT 3127; ♂, October 24, 1962, MCT 3137; sex?, November 1, 1962, MCT 3190; ♀, November 2, 1962, MCT 3201; ♀, November 11, 1962, MCT 3250; ♂ testis small, November 13, 1962, MCT 3271; ♀, November 17, 1962, MCT 3301. Oil Palm Research Station: ♀, August 16, 1963, ADG 246; ♀ juvenal, August 19, 1963, ADG 253; ♀, August 23, 1963, ADG 256; ♀, August 28, 1963, ADG 264; ♂, August 28, 1963, ADG 270; ♀, August 28, 1963, ADG 271; ♀, October 4, 1963, ADG 293.

At the Cocoa Research Station this species was common and inhabited the cocoa and surrounding secondary forest. I found it to be common 12 miles north of Kalabakan.

Criniger ochraceous ruficrissus Sharpe: Brown White-throated Bulbul.—*Specimens*, 5: 5.5 mi. SW Tenom: ♀, December 21, 1962, MCT 3489; ♂ testis 3 × 2 mm., December 21, 1962, MCT 3490; ♂ testis 4 × 3 mm., December 21, 1962, MCT 3491; ♀, December 23, 1962, MCT 3518; ♀, December 25, 1962, MCT 3535.

This bird was seen only in the moss forest above Tenom. It was not taken in nets the first four days they were erected, nor did we see individuals in the forest. Then, on December 21, three were taken in widely separated nets, and the species was then seen nearly every day for a week. Such sporadic and unpredictable local occurrences may indicate wide separation of the loosely-organized foraging groups of this species. The call is a harsh, jaylike note.

Criniger phaeocephalus connectens (Chasen and Kloss): Crestless White-throated Bulbul.—*Specimens*, 31: Cocoa Research Station: ♀, December 1, 1962, MCT 3406; ♂ testis 5 × 4 mm., 35.0 gm., July 31, 1962, MCT 2689; ♂, May 2, 1963, ADG 104; ♂, June 22, 1963, ADG 122. 12 mi. N Kalabakan: ♂ testis 6 × 4 mm., October 12, 1962, MCT 3002; ♀, October 12, 1962, MCT 3003; ♀, October 12, 1962, MCT 3004; ♂, October 14, 1962,

MCT 3037; ♂, October 14, 1962, MCT 3038; ♀, October 14, 1962, MCT 3039; ♀, October 17, 1962, MCT 3063; ♂, October 17, 1962, MCT 3071; ♂, October 19, 1962, MCT 3080; ♂, October 20, 1962, MCT 3106; ♂, October 20, 1962, MCT 3110; ♂, October 21, 1962, MCT 3115; ♀, October 22, 1962, MCT 3125; ♀, October 23, 1962, MCT 3135; ♀, October 24, 1962, MCT 3142; ♀, October 26, 1962, MCT 3155; ♂, October 28, 1962, MCT 3175; sex?, October 30, 1962, MCT 3186; ♀, November 1, 1962, MCT 3191; ♂, November 8, 1962, heavy molt, MCT 3234. Kalabakan: ♀, November 15, 1962, heavy molt, MCT 3288. 5.5 mi. SW Tenom: ♀, December 17, 1962, MCT 3453. Oil Palm Research Station: ♂, August 15, 1963, ADG 241; ♂, August 27, 1963, ADG 259; ♂, September 5, 1963, ADG 276. Gum-Gum: ♂, September 4, 1963, ADG 283. Lamag: ♂, October 15, 1963, ADG 308.

This species of the primary forest was common both at Cocoa Research Station and 12 miles north of Kalabakan. Although not frequently seen, it was caught in mist nets with regularity. Specimens taken near Kalabakan on November 8 and 15, 1962, were in heavy molt.

Criniger finschii Salvadori: Finsch's Bulbul.—*Specimens*, 9: Cocoa Research Station: ♂ testis 5 × 4 mm., 23.1 gm., August 23, 1962, MCT 2798; ♀, 24.4 gm., August 23, 1962, MCT 2799; ♂ testis 6 × 4 mm., 24.5 gm., September 13, 1962, MCT 2914; ♀, 24.0 gm., September 13, 1962, MCT 2915; ♂ testis 4 × 3 mm., September 24, 1962, MCT 2942; ♂ testis 6 × 5 mm., September 26, 1962, MCT 2969; ♀, September 27, 1962, MCT 2972; ♀, November 27, 1962, MCT 3341. 12 mi. N Kalabakan: ♀, October 19, 1962, heavy molt, MCT 3077.

This bulbul was common in the cocoa at the Cocoa Research Station. It fed in the company of other bulbuls in shade trees (*Trema orientalis*). The size of the testes of the males taken is characteristic of the beginning or ending of the breeding season, but ovaries of the females showed no signs of being in breeding condition.

According to Smythies (1960:385), this species had never been taken in North Borneo. These specimens, therefore, are the first recorded from there. Specimens previously were saved from Sarawak and Indonesian Borneo.

Hypsipetes criniger viridis (Bonaparte): Hairy-backed Bulbul.—*Specimens*, 26: Cocoa Research Station: ♂, September 26, 1962, MCT 2963; ♀, September 27, 1962, MCT 2971; ♀, November 27, 1962, MCT 3337; ♂, November 27, 1962, MCT 3356; ♀, July 7, 1963, ADG 169; ♂, June 14, 1963, ADG 139; ♂, June 12, 1963, ADG 125. 12 mi. N Kalabakan: ♀, October 13, 1962, MCT 3022; ♂, October 13, 1962, MCT 3023; ♀, October 13, 1962, MCT 3029; ♀, October 13, 1962, MCT 3033; ♂, October 14, 1962, MCT 3040; ♀, October 16, 1962, MCT 3054; ♂, October 16, 1962, MCT 3055; ♀, October 19, 1962, MCT 3081; ♀, October 19, 1962, MCT 3082; ♂, October 20, 1962, MCT 3109; ♂, October 22, 1962, MCT 3129; ♂, October 26, 1962, MCT 3162; ♂, November 11, 1962, MCT 3251; ♀, November 13, 1962, MCT 3273; ♀, November 13, 1962, MCT 3274; ♂, November 13, 1962, MCT 3275. Gum-Gum: ♀, October 3, 1963, ADG 288; ♂, October 3, 1963, ADG 289; ♂, August 12, 1963, ADG 228.

These bulbuls regularly feed on berries of *Trema orientalis*. I saw these bulbuls darting out after insects from branches, much as flycatchers would do, and have noticed a tendency toward flycatching in other bulbuls, but not so commonly as in this species. In using the name *Hypsipetes* instead of *Microscelis* I follow Rand and Rabor (1959:102).

Hypsipetes malaccensis Blyth: Streaked Bulbul.—*Specimens*, 4: Cocoa Research Station: ♂ testis 8 × 5 mm., 41.0 gm., August 20, 1962, MCT 2787. 12 mi. N Kalabakan: ♀, October 19, 1962, MCT 3092. 5.5 mi. SW Tenom: ♂, December 22, 1962, MCT 3497; ♂, December 22, 1962, MCT 3498.

I did not find this species common at any collecting locality. Smythies (1957:707) considered it a lowland species, but its occasional occurrence in the highlands is indicated by the specimen from Tenom.

Deignan (*in* Peters, 1960:291) regards *Hypsipetes virescens* and *Hypsipetes malaccensis* as specifically distinct.

Hypsipetes charlottae perplexus (Riley): Crested Olive Bulbul.—*Specimens,* 5: Cocoa Research Station: ♂ testis 5 × 3 mm., August 27, 1962, MCT 2818; ♂ testis 5 × 4 mm., September 25, 1962, MCT 2951; ♀, September 25, 1962, MCT 2952; ♂, November 27, 1962, MCT 3333; ♀ imm., 32.6 gm., July 22, 1962, MCT 2638.

This species was occasionally observed in the cocoa, where it fed on berries of *Trema orientalis.* The size of the testes in males taken in August suggests that the species had been breeding earlier.

Hypsipetes flavalus connectens (Sharpe): Ashy Bulbul.—*Specimens,* 7: 5.5 mi. SW Tenom: ♀, December 23, 1962, MCT 3508; ♀ largest ova 1 mm., December 17, 1962, MCT 3447; ♂, December 17, 1962, MCT 3448; ♂ testis 4 × 3 mm., December 19, 1962, MCT 3466; ♂, December 19, 1962, MCT 3467; ♂ testis 6 × 6 mm., December 20, 1962, MCT 3476; ♂ testis 5 × 4 mm., December 20, 1962, MCT 3477.

This was a common and conspicuous bird in the moss forest. Males called and sang there. The call note sounds like the mew of a cat. The Ashy Bulbul could easily be "squeaked in," at which time it approached silently. When observed in the forest it was noisy and gregarious.

Aegithina viridissima viridissima (Bonaparte): Green Iora.—*Specimens,* 7: Cocoa Research Station: ♀ largest ovum 1 mm., 13.5 gm., August 10, 1962, MCT 2755; ♂ testis 8 × 5 mm., 14.8 gm., August 10, 1962, MCT 2756; sex?, 13.2 gm., August 25, 1962, MCT 2805; ♂, 12.5 gm., September 10, 1962, MCT 2895; ♀, 13.0 gm., September 14, 1962, MCT 2921; ♀, November 27, 1962, MCT 3345. 5.5 mi. SW Tenom: ♂, December 20, 1962, MCT 3479.

In the cocoa this abundant bird usually occurred in flocks of five to 10 and fed 10 to 15 feet up in shade trees. On December 17, I saw singing males in the moss forest at 4,000 feet, 5.5 miles southwest of Tenom. This is considered a lowland species by Smythies (1957:698).

Aegithina tiphia aequanimis Bangs: Common Iora.—*Specimens,* 2: Tenom: ♂, January 5, 1963, MCT 3581; ♂, January 5, 1963, MCT 3582.

Two were netted in secondary forest near Tenom.

Chloropsis cyanopogon cyanopogon (Temminck): Lesser Green Leafbird.—*Specimens,* 8: Cocoa Research Station: ♀, 19.8 gm., July 21, 1962, MCT 2630; ♂ testis 2 × 1 mm., 25.3 gm., July 21, 1962, MCT 2631; ♂ testis 8 × 5 mm., August 27, 1962, MCT 2819; ♀, 22.2 gm., September 14, 1962, MCT 2923; ♀, November 27, 1962, MCT 3342; ♀, November 27, 1962, MCT 3352; ♀, April 28, 1963, ADG 77; ♀, May 28, 1963, ADG 116.

It was seen regularly in the cocoa at the research station and was the most common leafbird.

Chloropsis sonnerati zosterops Vigors: Greater Green Leafbird.—*Specimens,* 2: Cocoa Research Station: ♂ testis 3 × 2 mm., 45.8 gm., MCT 2707; ♂, 46.0 gm., August 8, 1962, MCT 2740.

It was seen many times in the cocoa.

Irena puella criniger Sharpe: Fairy Bluebird.—*Specimens,* 10: Cocoa Research Station: ♂ testis 3 × 1 mm., 63.6 gm., July 4, 1962, heavy molt, MCT 2588; ♀, 70.3 gm., July 28, 1962, MCT 2680; ♀, 69.8 gm., August 2, 1962,

MCT 2711; ♂ testis 13 × 10 mm., 65.0 gm., August 2, 1962, MCT 2714; sex?, August 2, 1962, MCT 2715; sex?, 64.5 gm., August 2, 1962, MCT 2716; ♀, June 15, 1963, ADG 143; ♀, July 11, 1963, ADG 189; ♀, June 27, 1963, ADG 163. Tiger Estate: ♂, June 23, 1963, ADG 157.

This was a common species around the Research Station in the cocoa and much-disturbed primary forest.

Erithacus cyane (Pallas): Siberian Blue Robin.—*Specimen,* 1: 12 mi. N Kalabakan: ♂, November 4, 1962, MCT 3208 (netted in primary forest).

Copsychus pyrrhopygus (Lesson): Orange-tailed Shama.—*Specimens,* 9: Cocoa Research Station: ♂ testis 3 × 2 mm., July 11, 1962, MCT 2617; ♂, September 7, 1962, MCT 2885; ♀, October 3, 1962, MCT 2985; ♂, December 1, 1962, MCT 3401; ♂, November 30, 1962, MCT 3444. 12 mi. N Kalabakan: ♂ testis 5 × 3 mm., October 14, 1962 MCT 3044; ♀, November 13, 1962, MCT 3272. Oil Palm Research Station: ♂, June 20, 1963, ADG 154; ♀, August 11, 1963, ADG 222.

This bird of the primary forest was only rarely seen in secondary forest. The specimen taken on July 11, 1962, was in heavy molt with only two outermost tail feathers in evidence; there was also molt of the wing and body feathers.

Copsychus saularis pluto Bonaparte: Magpie-Robin.—*Specimens,* 3: Pintasan Agriculture Station: ♂, October 18, 1963, ADG 323. Tuaran: ♀, December 14, 1963, SCFC 219. Telipok: ♀, March 9, 1963, TM 68.

This species was recorded at Tawau in cultivated areas but no specimens were collected there. Those collected by Garcia, Chung, and Conway tended to be morphologically intermediate between *C. s. adamsi* and *C. s. pluto.*

Copsychus stricklandi stricklandi Motley and Dillwyn: White-rumped Shama.—*Specimens,* 14. Cocoa Research Station: ♂ testis 8 × 5 mm., August 28, 1962, MCT 2826; ♂ testis 11 × 6 mm., September 5, 1962, MCT 2873; ♀, November 28, 1962, MCT 3359; ♀, November 29, 1962, MCT 3389. 12 mi. N Kalabakan: ♂, October 12, 1962, MCT 3012; ♀, October 12, 1962, MCT 3013; ♀ brood patch, oviduct enlarged, October 17, 1962, MCT 3069; ♀, October 19, 1962, MCT 3078; ♀, October 26, 1962, MCT 3154. 5.5 mi. SW Tenom: ♂, December 23, 1962, MCT 3514. Ulu Balung Cocoa Estate: ♂, July 15, 1963, ADG 200. Oil Palm Research Station: ♀, August 27, 1963, ADG 263; ♀, August 28, 1963, ADG 268; ♀, October 4, 1963, ADG 291.

This species was common in the cocoa and surrounding secondary forest at Quoin Hill, but I saw it only once in the moss forest on the mountains near Tenom.

No specimen taken showed characters of or tendencies toward *C. malabaricus suavis.* Perhaps the zone of intergradation on the east coast is farther south than Darval Bay, where it was placed by Smythies (1960:390).

S. D. Ripley (*in* Peters *et al.,* 1964:72) considered *C. stricklandi* to be specifically distinct from *C. malabaricus,* and his opinion is accepted here.

Enicurus leschenaulti borneensis Sharpe: White-crowned Forktail. *Specimens,* 4: 12 mi. N Kalabakan: ♀ imm., October 21, 1962, MCT 3112; ♀ largest ovum 2 mm., October 27, 1962, MCT 3167; ♂, November 1, 1962, MCT 3195. Gum-Gum: ♀, September 24, 1963, ADG 282.

I saw this species only once in life, along a small, wet-weather stream. The specimens, however, were all netted in primary forest, some distance away from any stream.

Judging from measurements, these specimens are *E. l. borneensis*, although one would expect to find only *E. l. frontalis* at elevations of 600 feet. The specimen taken by Garcia at Gum-Gum was not identified to subspecies.

Enicurus ruficapillus Temminck: Chestnut-naped Forktail.—*Specimens*, 3: 12 mi. N Kalabakan: ♂, October 21, 1962, MCT 3113; ♂, November 4, 1962, MCT 3207; ♂, November 8, 1962, MCT 3231.

This bird was common along the upper Apas River at Quoin Hill. All specimens were taken in nets stretched across streams.

Zoothera interpres interpres (Temminck): Chestnut-headed Ground Thrush.—*Specimens*, 9: 12 mi. N Kalabakan: ♀, October 28, 1962, MCT 3171; ♀, October 24, 1962, MCT 3138. Kalabakan: ♀, November 17, 1962, MCT 3300. Cocoa Research Station: ♀ imm., June 10, 1963, ADG 120; ♂, June 12, 1963, ADG 130; ♀ imm., June 15, 1963, ADG 141. Oil Palm Research Station: ♂, August 15, 1963, ADG 233; ♂, August 9, 1963, ADG 217; ♂, August 27, 1963, ADG 261.

The many specimens of this species taken indicate the effectiveness of mist nets in collecting birds in tropical forest. Although Smythies (1960:398) considered this bird to be rare in Borneo, I think that it is merely shy and retiring. We never saw the species in the field and the specimens were all netted. The habitat was in primary forest, except for that of MCT 3300, which was taken in dense secondary forest. The two birds from 12 miles north of Kalabakan were taken in a net stretched across a surveyor's transect. The net was set on a hilltop and the birds hit it approximately three feet above the ground. Two of the specimens from the Cocoa Research Station are in juvenal plumage, indicating that this species probably breeds in the area.

Cettia whiteheadi (Sharpe): Short-tailed Bush Warbler.—*Specimen*, 1: 5.5 mi. SW Tenom: ♂ testis 3 × 2 mm., December 21, 1962, MCT 3488.

The specimen was netted in the moss forest, in fairly heavy secondary undergrowth.

Prinia flaviventris (Delessert): Yellow-bellied Wren-Warbler.—On September 2, 1962, I saw several of these wren-warblers in a grassy area near the golf course at Tawau.

Acrocephalus arundinaceus orientalis (Temminck and Schlegel): Great Reed Warbler.—*Specimens*, 6: Tenom: ♀, December 31, 1962, MCT 3546; ♂, January 1, 1963, MCT 3555; ♂, January 2, 1963, MCT 3565; ♀, January 4, 1963, MCT 3575; ♀, January 3, 1963, MCT 3574; ♂, January 4, 1963, MCT 3579.

This species was common in the old paddy near Tenom, which has now grown up to grass and shrubs. I saw one individual also in shrubbery in Jesselton.

Phylloscopus borealis (Blasius): Arctic Leaf Warbler.—I saw this leaf warbler once in dense scrub in the moss forest near Tenom.

Seicercus superciliaris schwaneri (Blyth): White-throated Flycatcher Warbler.—*Specimens*, 2: 5.5 mi. SW Tenom: ♂ testis 4 × 2 mm., December 23, 1962, MCT 3510; ♀, December 23, 1962, MCT 3511.

In the moss forest this was a common bird that hopped about in the climbing bamboo and scrub.

Orthotomus atrogularis humphreysi Chasen and Kloss: Black-necked Tailorbird.—*Specimens*, 5: Cocoa Research Station: ♂ testis 4 × 2 mm., 6.5 gm.,

August 28, 1962, MCT 2827; ♀ oviduct enlarged, brood patch, 5.5 gm., August 28, 1962, MCT 2828; ♂ testis 4 × 2 mm., September 26, 1962, MCT 2967; ♀, November 27, 1962, MCT 3336; ♀, November 28, 1962, MCT 3375.

These birds lived in the secondary forest-edge in dense shrubbery. They were breeding at a time when most other birds seemed to have completed breeding activities; most had begun the post-breeding (prealternate) molt. On October 3, 1962, I saw two adults with two young in nondescript juvenal plumage with virtually no markings and a pale yellow color, unlike that of the adults.

Orthotomus sericeus sericeus Temminck: Red-headed Tailorbird.—*Specimens*, 1: Cocoa Research Station: ♀ with large ovum, 10.8 gm., August 11, 1962, MCT 2770.

The bird was uncommon at the research station. The one specimen was from the cocoa. I saw two others in secondary growth on the edge of the forest. Possibly this species, like the preceding one, was approaching full breeding activity.

Orthotomus sepium borneonensis Salvadori: Ashy Tailorbird.—*Specimens*, 8: Cocoa Research Station: ♀ vascular brood patch, oviduct enlarged with one possible collapsed follicle, 7.8 gm., August 22, 1962, MCT 2797; ♀ imm., 8.0 gm., August 28, 1962, MCT 2829; ♂, 8.8 gm., September 10, 1962, MCT 2896; ♂, 8.5 gm., September 10, 1962, MCT 2897; ♂ testis 5 × 3 mm., 8.5 gm., September 11, 1962, MCT 2901; ♀ largest ova 3 mm., 8.5 gm., September 11, 1962, MCT 2902. Tiger Estate: ♀, October 11, 1962, MCT 3000. 5.5 mi. SW Tenom: ♀, December 20, 1962, MCT 3486.

This was the most common tailorbird in the Quoin Hill area. Indications were that the species was also breeding (see *O. sericeus*). Besides the above localities, I observed it 12 miles north of Kalabakan. A male was heard singing on September 11, 1962; the song was simple and on an ascending scale. The specimen taken near Tenom was growing new tail feathers.

Rhipidura perlata S. Müller: Spotted Fantail Flycatcher.—*Specimens*, 19: Cocoa Research Station: ♀ largest ova 2 mm., July 11, 1962, MCT 2618; ♂ testis 6 × 5 mm., 15.1 gm., July 23, 1962, MCT 2645; ♀, 13.2 gm., August 13, 1962, MCT 2776; ♀, 12.4 gm., August 20, 1962, MCT 2785; ♂, June 12, 1963, ADG 129. 12 mi. N Kalabakan: ♂, October 13, 1962, MCT 3021; ♂, October 16, 1962, MCT 3056; ♀, October 16, 1962, MCT 3057; ♂, October 16, 1962, MCT 3111; ♀, October 24, 1962, MCT 3141; ♂, October 24, 1962, MCT 3146; ♂, October 24, 1962, MCT 3148; sex?, October 26, 1962, MCT 3165; ♂, October 27, 1962, MCT 3168; ♂, October 27, 1962, MCT 3169; sex?, October 30, 1962, MCT 3197. Ulu Balung Cocoa Estate: ♀, July 13, 1963, ADG 198; ♀, July 24, 1963, ADG 214. Oil Palm Research Station: sex?, August 15, 1963, ADG 243.

This bird was one of the most common in the lower story of the primary forest. On July 23, 1962, many males were performing courtship displays at Quoin Hill.

Rhipidura javanica longicauda Wallace: Pied Fan-tailed Flycatcher.—*Specimens*, 3: Tawau: sex?, September 2, 1962, MCT 2863. Telipok: ♀, February 9, 1963, TM 28. Tuaran: sex?, December 14, 1963, SCFC 19.

On Karindingen Island this was the only passerine bird seen. It was confined to the lowlands and never was seen in localities more than a few feet above sea level.

Culicicapa ceylonensis ceylonensis (Swainson): Gray-headed Flycatcher.—*Specimens*, 6: Cocoa Research Station: ♂, 8.0 gm., August 4, 1962, MCT

2726; sex?, August 20, 1962, 8.6 gm., MCT 2784. 12 mi. N Kalabakan: ♀?, October 12, 1962, MCT 3018; ♂, October 13, 1962, MCT 3024; ♂ testis 4 × 4 mm., October 28, 1962, MCT 3179. 5.5 mi. SW Tenom: ♂, December 20, 1962, MCT 3483.

This bird of the primary forest and primary-secondary forest ecotone was common at all three principal collecting stations.

Muscicapa sibirica Gmelin: Sooty Flycatcher.—*Specimens*, 2: Cocoa Research Station: ♂, 10.0 gm., August 25, 1962, MCT 2811; ♂, July 8, 1963, ADG 174.

Several small "brown" flycatchers which could not be assigned to species were observed at Quoin Hill and Kalabakan. The specimen taken by Garcia is of interest as it was taken on a date extremely early for a migrant. Garcia's specimen (not the other) also presented problems of identification and its assignment to this species is tentative.

Muscicapa latirostris latirostris Raffles: Brown Flycatcher.—*Specimen*, 1: Cocoa Research Station: ♀, September 26, 1962, MCT 2965.

Muscicapa cyanomelana cyanomelana Temminck: Blue and White Flycatcher.—*Specimen*, 1: Cocoa Research Station: ♂, November 27, 1962, MCT 3335.

The specimen, netted in the cocoa, apparently provides the only record from the east coast of Borneo (see Smythies, 1957:742).

Muscicapa concreta everetti (Sharpe): White-tailed Blue Flycatcher.—*Specimens*, 6: 12 mi. N Kalabakan: ♂, October 15, 1962, MCT 3045; ♂, November 1, 1962, MCT 3199; ♀, November 8, 1962, MCT 3229; ♂, November 8, 1962, MCT 3230. 5.5 mi. SW Tenom: ♂, December 19, 1962, MCT 3465; ♀, December 23, 1962, MCT 3516.

This species seems to be confined to the primary forest, and was common at both localities listed. Smythies (1960:444) thought it resided primarily at elevations of 2,000 to 4,000 feet, occasionally occurring near sea level. This flycatcher seems to prefer the understory of the forest, where it was observed sitting on bare limbs and darting out after insects.

Muscicapa unicolor infuscata (Hartert): Pale Blue Flycatcher.—*Specimens*, 2: 12 mi. N Kalabakan: ♂ by plumage, October 31, 1962, MCT 3189; ♀, November 12, 1962, MCT 3556.

This flycatcher was seen only in primary forest, on the above dates. The birds collected appear to provide the only definitive records for North Borneo (*cf.* Symthies, 1960:445), although Mary Norman observed the species once at Quoin Cocoa Estate on an unspecified date (Smythies, 1963:281).

Muscicapa turcosa rupatensis Oberholser: Malaysian Blue Flycatcher.—*Specimen*, 1: Tiger Estate: ♀, November 25, 1962, MCT 3320.

Muscicapa caerulata caerulata (Bonaparte): Large-billed Blue Flycatcher.—*Specimens*, 10: Ulu Balung Cocoa Estate: ♂, July 10, 1963, ADG 185. 12 mi. N Kalabakan: ♂, October 19, 1962, MCT 3076; ♂, October 24, 1962, MCT 3144; ♂, October 26, 1962, MCT 3160; ♀, October 28, 1962, MCT 3170; ♀, November 8, 1962, MCT 3232; ♂, November 13, 1962, MCT 3266. Oil Palm Research Station: ♀, August 12, 1963, ADG 223; ♀, August 16, 1963, ADG 244; ♂, August 19, 1963, ADG 252.

This was the most common "blue" flycatcher at Kalabakan. It was recorded at Quoin Hill only by Garcia. The record by Smythies (1963:281) seems open to question as no specimen was preserved.

Muscicapa venusta Deignan: Bornean Blue Flycatcher.—*Specimens*, 6: Cocoa Research Station: ♂, September 24, 1962, MCT 2939; ♂, June 12, 1963, ADG 128. 12 mi. N Kalabakan: ♂, October 12, 1962, MCT 3014; ♂, October 19, 1962, MCT 3089. Oil Palm Research Station: ♀, August 10, 1963, ADG 218. Kinabatangan: sex?, October 15, 1963, ADG 309.

The "blue" flycatcher of the Quoin Hill area was observed several times in the primary forest and primary forest edge. On July 14, 1962, I saw a male and a female of *M. venusta* bathing in a shallow stream in the deep forest. They fluttered their wings in the water and then flew to a nearby fallen log and preened for several minutes.

Muscicapa rufigastra rufigastra Raffles: Mangrove Blue Flycatcher.—*Specimen*, 1: Tuaran: ♂, December 14, 1963, SCFC 33.

Muscicapa dumetoria mulleri Blyth: Orange-breasted Flycatcher.—*Specimens*, 5: Cocoa Research Station: ♂, 11.8 gm., July 25, 1962, MCT 2661; ♀, November 1, 1962, MCT 3198; ♂ testis 3 × 2 mm., November 11, 1962, MCT 3246; ♂ testis 5 × 4 mm., November 28, 1962, MCT 3384. 5.5 mi. SW Tenom: ♂, December 25, 1962, MCT 3531.

This species was seen only in the understory of primary forest. On November 10, I watched a male and female feeding about three feet above the ground in the undergrowth. They sat on small vines and plants and darted out after insects. I never observed this species more than 20 feet above the ground.

Muscicapa narcissina Temminck: Black and Yellow Flycatcher.—*Specimens*, 2: Cocoa Research Station: ♀, November 27, 1962, MCT 3331. 5.5 mi. SW Tenom: ♂, December 20, 1962, MCT 3484.

The two specimens were taken in nets in the primary forest. They cannot presently be assigned with certainty to subspecies.

Rhinomyias umbratilis (Strickland): White-throated Jungle Flycatcher.—*Specimens*, 19: Cocoa Research Station: ♀, 16.7 gm., July 25, 1962, MCT 2662; ♂ testis 6 × 5 mm., 20.7 gm., July 25, 1962, MCT 2663; ♀, 17.9 gm., July 31, 1962, MCT 2686; ♀, September 29, 1962, MCT 2974; ♂, July 8, 1963, ADG 175. 12 mi. N Kalabakan: ♂, October 10, 1962, MCT 2993; ♀, October 13, 1962, MCT 3027; ♂, October 13, 1962, MCT 3031; ♂, October 14, 1962, MCT 3036; ♂, October 16, 1962, MCT 3053; ♂, October 16, 1962, MCT 3058; ♂, October 18, 1962, MCT 3074; ♀, October 20, 1962, MCT 3107; ♂, October 23, 1962, MCT 3132; ♂, October 25, 1962, MCT 3149; ♀, October 28, 1962, MCT 3174. Ulu Balung Cocoa Estate: ♀, July 11, 1963, ADG 195; ♀, July 12, 1963, ADG 196; ♀, July 19, 1963, ADG 212.

This abundant species at Quoin Hill and Kalabakan was chiefly an inhabitant of primary forest.

On July 31, I observed this species singing at Quoin Hill. One sang with its mouth closed and sounded much farther away than it actually was. The song has seven notes on a descending scale. Birds observed on September 27 were in heavy molt and one specimen lacked tail feathers.

Philentoma pyrrhoptera pyrrhoptera (Temminck): Chestnut-winged Monarch Flycatcher.—*Specimens*, 10: 12 mi. N Kalabakan: ♂, October 10, 1962, MCT 2992; ♀, October 15, 1962, MCT 3048; ♂, October 20, 1962, MCT 3100; ♂, October 20, 1962, MCT 3105; ♀, November 11, 1962, MCT 3244; ♀, November 16, 1962, MCT 3291. Ulu Balung Cocoa Estate: ♂, July 9, 1963, ADG 180; ♂, July 9, 1963, ADG 181; ♂, July 24, 1963, ADG 215; ♀, July 11, 1963, ADG 192.

The species was common at Kalabakan. Garcia took a few at Quoin Hill, but I observed the species there only once.

Philentoma velata caesia (Lesson): Maroon-breasted Monarch Flycatcher.—*Specimens,* 7: Cocoa Research Station: ♀, 25.0 gm., August 4, 1962, MCT 2725; ♂, 27.2 gm., August 20, 1962, MCT 2783; ♂, September 5, 1962, MCT 2872. 12 mi. N Kalabakan: ♀, October 22, 1962, MCT 3126; sex? (♀ by plumage), October 29, 1962, MCT 3182; ♀, November 3, 1962, MCT 3205. 5.5 mi. SW Tenom: ♂, December 26, 1962, MCT 3536.

At Quoin Hill this was a bird of the primary forest. The species was common in the moss forest above Tenom.

Hypothymis azurea prophata Oberholser: Black-naped Blue Monarch Flycatcher.—*Specimens,* 18: Cocoa Research Station: ♀, 10.8 gm., August 10, 1962, MCT 2754; ♂, 15.2 gm., August 28, 1962, MCT 2834; ♂ testis 6 × 4 mm., 11.1 gm., September 6, 1962, MCT 2876; sex? September 14, 1962, MCT 2922; ♂, November 1, 1962, MCT 3200; ♂, November 7, 1962, MCT 3221; ♂, November 10, 1962, MCT 3242; ♂, November 20, 1962, MCT 3373; ♀, November 28, 1962, MCT 3374; ♂ testis 5 × 3 mm., December 1, 1962, MCT 3412; ♀, December 2, 1962, MCT 3427. 5.5 mi. SW Tenom: ♂, December 22, 1962, MCT 3504; ♂, December 23, 1962, MCT 3509. Cocoa Research Station: ♀, April 30, 1963, ADG 95; ♀, June 19, 1963, ADG 1551. Ulu Balung Cocoa Estate: ♂, July 11, 1963, ADG 194; Oil Palm Research Station: ♂, August 10, 1963, ADG 220; ♀, August 13, 1963, ADG 232.

This seemingly ubiquitous bird occurred in primary forest and cocoa. A specimen taken on September 14, 1962, was still in heavy molt.

Terpsiphone paradisi borneensis (Hartert): Paradise Flycatcher.—*Specimens,* 6: Cocoa Research Station: ♂ testis 9 × 5 mm., July 11, 1962, MCT 2616; ♂ testis 2 × 1 mm., 21.2 gm., August 3, 1962, MCT 2719; ♀, June 10, 1963, ADG 119. 12 mi. N Kalabakan: ♂, October 19, 1962, MCT 3090; ♀, November 10, 1962, MCT 3240. Oil Palm Research Station: ♀, August 24, 1963, ADG 258.

At Quoin Hill this species was common in primary forest. One of the males (MCT 2719) was rust-colored. It and similar rufous males may be immature (see Owen, 1963:235).

Pachycephala whiteheadi homeyeri (Blasius): Whitehead's Thick-head.—*Specimens,* 2: Siamil Island: ♀, September 19, 1962, MCT 2931; ♂, September 19, 1962, MCT 2932.

The thick-heads were by far the most common passerine bird in the relict forest on Siamil Island, being quite tame and easily approached. They generally spent most of their time sitting on branches of forest vines and bushes in the understory and were never observed in the upper story. McGregor (1910:604) describes the species as: "Common on Tawi Tawi, less so in Sulu. A deep woods bird; tame and easily shot. Feeds on insects, and usually keeps some distance above the ground."

The two specimens recorded above provide the first record of this species from Borneo, the previously known range being confined to the Philippine Islands. My material closely resembled the subspecies found on Tawi-Tawi and here is assigned to *P. w. homeyeri.*

Motacilla caspica melanope Pallas: Gray Wagtail.—*Specimen,* 1: Cocoa Research Station: ♀, October 4, 1962, MCT 2991.

I saw this migrant first at the research station on August 25, 1962, along a dirt road, and it was subsequently seen many times along logging roads in secondary forest.

Artamus leucorhynchus leucorhynchus Linnaeus: White-breasted Swallow Shrike.—*Specimens,* 2: Tuaran: sex?, December 6, 1963, SCFC F13; ♀, December 7, 1963, SCFC F15.

Lanius cristatus lucionensis Linnaeus: Brown Shrike.—*Specimen,* 1: Tuaran: ♂, January 12, 1963, MCT 3593.

One bird was observed near our sulap 12 miles north of Kalabakan on October 22 and 26, 1962. The specimen was netted in a paddy field and others were seen at Tuaran.

Lanius tigrinus Drapiez: Thick-billed Shrike.—*Specimens,* 2: Tiger Estate: ♂, November 25, 1962, MCT 3316. Cocoa Research Station: ♀, November 29, 1962, MCT 3383.

The specimen taken on November 29, was netted in a small clearing in primary forest.

Aplonis panayensis strigatus (Horsfield): Glossy Starling.—*Specimens,* 2: Tiger Estate: ♀, October 11, 1962, MCT 3001; ♀, November 25, 1962, MCT 3322. Tuaran: ♀, March 21, 1963, ADG 35; sex?, December 1, 1963, EJHB 616.

This species was in the lowlands around Semporna, Siamil Island, Brantian Estate, and Tawau.

Gracula religiosa religiosa Linnaeus: Talking Myna.—*Specimens,* 3: Tiger Estate: ♀, October 11, 1962, MCT 3020. Cocoa Research Station: ♂, May 28, 1963, ADG 114. Gum-Gum: ♀, September 9, 1963, ADG 277.

This was a common bird at Quoin Hill but was not seen elsewhere by me. It frequented the dead trees in the cocoa.

Anthreptes simplex (S. Müller): Plain-colored Sunbird.—*Specimens,* 6: Cocoa Research Station: ♀ imm., 8.0 gm., August 11, 1962, MCT 2768; ♂ imm., 10.0 gm., August 11, 1962, MCT 2769; ♂, 7.0 gm., September 6, 1962, MCT 2878; ♂, September 25, 1962, MCT 2959; ♀, November 27, 1962, MCT 3332; ♂, November 27, 1962, MCT 3343.

This common bird at Quoin Hill frequented flowers of the Tree Cassava. Trees of that species were shade trees in the cocoa.

Anthreptes malacensis ssp. (Scopoli): Brown-throated Sunbird.—*Specimens,* 2: Tenom: ♂, January 3, 1963, MCT 3573; ♂ testis 5 × 4 mm., January 4, 1963, MCT 3576.

One of the specimens (MCT 3576) was molting into adult male plumage; the size of its testes suggests that this bird was also coming into breeding condition, all of which seemingly lends support to Chasen's (1939:401) suspicion that the species has an eclipse plumage. Lacking specimens in breeding plumage, I was unable to determine the subspecific affinities of the population at Tenom.

This species was observed also on Siamil Island.

Anthreptes rhodolaema Shelley: Rufous-throated Sunbird.—*Specimens,* 14: Cocoa Research Station: ♂ testis 3 × 3 mm., 12.5 gm., August 9, 1962, MCT 2742; ♂ testis 5 × 3 mm., 15.0 gm., August 9, 1962, MCT 2743; ♀, 13.5 gm., August 9, 1962, MCT 2744; ♀ imm., 12.7 gm., August 9, 1962, MCT 2745; ♂ testis 3 × 2 mm., 13.5 gm., August 10, 1962, MCT 2749; ♂, 13.0 gm., August 10, 1962, MCT 2750; ♀, 12.0 gm., August 10, 1962, MCT 2751; ♀ imm., 10.8 gm., August 13, 1962, MCT 2775; ♂, September 4, 1962, MCT 2869; ♀ largest ova 3 mm., oviduct enlarged, 12.0 gm., September 12, 1962, MCT 2905; ♀, November 27, 1962, MCT 3350; ♂, November 27, 1962, MCT 3351; ♂, November 27, 1962, MCT 3355.

The Rufous-throated Sunbirds were the most common sunbirds at the Cocoa Research Station. They seemed to prefer foraging about flowers of the Tree Cassava. The stomachs of those examined contained insects. The absence of *A. malacensis* suggests that these two species are mutually exclusive.

Anthreptes singalensis borneana (Kloss): Ruby-cheeked Sunbird.—*Specimens,* 3: Cocoa Research Station: ♂, 8.0 gm., August 23, 1962, MCT 2801; ♂, November 29, 1962, MCT 3385; ♀, 8.4 gm., August 10, 1962, MCT 2752.

This species seemed to prefer secondary forest or cocoa as a habitat and was an uncommon bird at Quoin Hill.

Nectarinia sperata (Linnaeus): Van Hasselt's Sunbird.—Fred Dunn saw a male in secondary forest near the Cocoa Research Station.

Nectarinia jugularis (Linnaeus): Yellow-breasted Sunbird.—This sunbird was abundant in the coconut palms at Siamil Island. The species was observed also at exotic flowering plants in Tawau.

Nectarinia hypogrammica hypogrammica S. Müller: Purple-naped Sunbird.—*Specimens,* 10: Cocoa Research Station: ♀, November 27, 1962, MCT 3334; ♂, July 7, 1963, ADG 167. 12 mi. N Kalabakan: ♂ testis 3 × 5 mm., October 14, 1962, MCT 3035; ♂, October 15, 1962, MCT 3047; ♂, October 23, 1962, MCT 3133; ♂, October 24, 1962, MCT 3145; ♂, November 2, 1962, MCT 3203; ♀, November 15, 1962, MCT 3287. Oil Palm Research Station: ♀, August 16, 1963, ADG 247; ♂, August 27, 1963, ADG 262.

This common species of secondary forest at Quoin Hill seems to prefer spiders and various insects for food. I saw one bird removing dead leaves from a tree and picking out the spiders that had taken over the curled leaves as shelters. I also saw birds of this species hover before spiderwebs and remove the spiders.

A specimen taken on November 15, 1962, was in heavy molt.

Aethopyga mystacalis (Temminck): Scarlet Sunbird.—*Specimen,* 1: Cocoa Research Station: ♂, 6.0 gm., September 12, 1962, MCT 2903.

This specimen was molting from a drab to an adult type male plumage. I saw this species only one other time at Quoin Hill, but on December 26 I saw two males feeding among epiphytic plants in the moss forest above Tenom. The condition of the specimen's plumage prevented its identification to subspecies (presumably *A. m. temmincki*).

Aethopyga siparaja (Raffles): Yellow-backed Sunbird.—*Specimens,* 3: Tawau: ♂ testis 5 × 5 mm., September 2, 1962, MCT 2861. Tiger Estate: ♂, October 11, 1962, MCT 2999. Oil Palm Research Station: ♀, August 13, 1963, ADG 231.

This sunbird was common around flowers at Kalabakan and Brantian Estate.

Unfortunately, I lack enough specimens to make a subspecific identification. The specimen from Tawau differs from *A. s. siparaja,* however, only in having darker wings; it closely resembles the type and the series that Oberholser used when describing *A. s. ochrapyrrha.*

Arachnothera longirostris buttikoferi van Oort: Little Spiderhunter.—*Specimens,* 58: Cocoa Research Station: ♂, 16.2 gm., August 13, 1962, MCT 2777; ♂, 15.6 gm., August 22, 1962, MCT 2796; ♂ testis 6 × 4 mm., 16.0 gm., September 13, 1962, MCT 2913; ♀, December 1, 1962, MCT 3399; ♂ testis 4 × 3 mm., December 2, 1962, MCT 3431; ♂, November 27, 1962, MCT 3347; ♀, November 27, 1962, MCT 3348; ♂, November 28, 1962,

MCT 3366; ♂, November 28, 1962, MCT 3367; ♀, November 28, 1962, MCT 3368; ♀, November 28, 1962, MCT 3369; ♂, November 28, 1962, MCT 3370; ♀, November 28, 1962, MCT 3371; ♂, November 28, 1962, MCT 3372; ♂, November 29, 1962, MCT 3386; ♂, December 1, 1962, MCT 3397; ♂, December 1, 1962, MCT 3398; ♀, December 2, 1962, MCT 3430; ♀?, November 30, 1962, MCT 3443; ♀, April 26, 1962, ADG 60; ♂, April 27, 1963, ADG 70; ♂, April 27, 1962, ADG 73; ♂, April 18, 1963, ADG 78; ♂, April 28, 1963, ADG 80; ♂, April 29, 1963, ADG 86; ♂, April 29, 1963, ADG 87; ♂, April 30, 1962, ADG 93. 12 mi. N Kalabakan: ♀, October 16, 1962, MCT 3050; ♂, October 16, 1962, MCT 3051; ♂ testis 4 × 2 mm., October 18, 1962, MCT 3073; ♀, October 17, 1962, MCT 3064; ♂ testis 7 × 5 mm., October 19, 1962, MCT 3079; ♀, October 19, 1962, MCT 3093; ♂, October 21, 1962, MCT 3120; ♂, October 23, 1962, MCT 3134; ♂ testis enlarged, October 25, 1962, MCT 3150; ♂ testis 7 × 5 mm., October 26, 1962, MCT 3156; ♀, October 28, 1962, MCT 3173; ♂, November 2, 1962, MCT 3204; ♂, November 4, 1962, MCT 3209; ♂ testis 5 × 4 mm., November 4, 1962, MCT 3210; ♂ testis 2 × 1 mm., November 6, 1962, MCT 3214; ♀, November 11, 1962, MCT 3252. Kalabakan: ♀, November 15, 1962, MCT 3278; ♀ 2 eggs in oviduct, ovary enlarged, brood patch, November 15, 1962, MCT 3279; ♀ brood patch, two collapsed follicles, November 15, 1962, MCT 3280; ♂ testis 7 × 6 mm., November 15, 1962, MCT 3281; ♀ brood patch, egg in oviduct, largest ovum 6 mm., November 15, 1962, MCT 3286; ♂ testis 7 × 6 mm., November 16, 1962, MCT 3290; ♂ testis 3 × 2 mm., November 16, 1962, MCT 3294; ♀, November 16, 1962, MCT 3295; ♂ testis 6 × 3 mm., November 17, 1962, MCT 3297; ♂ testis 5 × 5 mm., November 17, 1962, MCT 3298; ♀, November 17, 1962, MCT 3299. 5.5 mi. SW Tenom: ♀, December 26, 1962, MCT 3538. Gum-Gum: ♂, October 4, 1963, ADG 290; ♀, October 5, 1963, ADG 294; ♀, October 5, 1963, ADG 295.

This was the most common of all the spiderhunters, and was found at all localities. It was readily taken in mist nets. Unlike most birds, these spiderhunters become quite agitated in nets, and within a few minutes usually strangle themselves.

From October 16 through November 11, I took several specimens 12 miles north of Kalabakan, but only one in breeding condition. On November 15, I moved 12 miles back to Kalabakan from an elevation of 600 feet to an elevation of 50 feet. As can be seen from the specimen-data, nearly all the females then collected either had nests with eggs or were approaching oviposition. The specimens were all taken in nets in an area approximately 200 feet square. On November 20 at the Brantian Estate a bird sitting on a branch six inches up in secondary forest jumped down to the ground and fed on unknown material.

Arachnothera crassirostris (Reichenbach): Thick-billed Spiderhunter.—*Specimen,* 1: Cocoa Research Station: ♀, 14.8 gm., August 9, 1962, MCT 2746.

This spiderhunter was recorded on the basis of one specimen and one sight record. One seen in secondary forest would dart out from its perch on a limb, hover near the end of a branch, and then return to its perch. No flowers were visible and I assumed that the bird was catching insects.

Arachnothera flavigaster (Eyton): Greater Yellow-eared Spiderhunter.—*Specimens,* 9: Cocoa Research Station: ♀ imm., 36.3 gm., August 21, 1962, MCT 2789; ♀ imm., 38.4 gm., August 21, 1962, MCT 2790; ♀, 38.4 gm., August 22, 1962, MCT 2795; ♀ brood patch, largest ova 2 mm., November 27, 1962, MCT 3330; ♂, November 28, 1962, MCT 3359; ♂ testis 7 × 6 mm., November 29, 1962, MCT 3379; ♂, November 30, 1962, MCT 3395; ♀, April 27, 1963, ADG 66; ♀, April 27, 1963, ADG 67.

This species was met with only at Quoin Hill, where it was common around the abaca and wild bananas. The primary diet seemed to be pollen, nectar, and spiders. I found it easy to differentiate from the next species in the field (see below).

Arachnothera chrysogenys harrissoni Deignan: Lesser Yellow-eared Spiderhunter.—*Specimens,* 4: Cocoa Research Station: ♀, 23.5 gm., August 21, 1962, MCT 2788; ♂, April 27, 1963, ADG 68; ♂, April 30, 1963, ADG 92; ♂, May 27, 1963, ADG 113.

I observed this species at Quoin Hill only once, but Garcia took three specimens at the same locality. He labels his specimens as taken in primary forest. I never saw the species there and took my one specimen in the abaca, where the bird was eating spiders, nectar, and pollen. The chief characters distinguishing this species from *A. flavigaster* were the tuft of yellow feathers on the side of the head and the narrow eye ring in *A. chrysogenys.*

Arachnothera affinis pars Riley: Gray-breasted Spiderhunter.—*Specimens,* 27: Cocoa Research Station: ♂, 27.2 gm., August 13, 1962, MCT 2771; ♀, 22.2 gm., August 13, 1962, MCT 2772; ♀ imm., 21.1 gm., August 13, 1962, MCT 2773; ♂, 29.2 gm., August 13, 1962, MCT 2774; ♂, 27.0 gm., August 21, 1962, MCT 2791; ♂, 26.6 gm., August 21, 1962, MCT 2792; ♂, April 27, 1963, ADG 65; ♀ imm., May 1, 1963, ADG 99; ♂, June 12, 1963, ADG 126; ♂, June 20, 1963, ADG 154-B. 12 mi. N Kalabakan: ♀, October 15, 1962, MCT 3046; ♀, October 24, 1962, MCT 3139. Cocoa Research Station: ♂ testis 3 × 2 mm., November 27, 1962, MCT 3327; ♀, November 27, 1962, MCT 3328; ♀, November 27, 1962, MCT 3329; ♀, November 27, 1962, MCT 3338; ♂ testis 5 × 4 mm., November 27, 1962, MCT 3339; ♂, November 28, 1962, MCT 3363; ♀, November 28, 1962, MCT 3364; ♂, November 28, 1962, MCT 3365; ♀, November 28, 1962, MCT 3366; ♀, November 29, 1962, MCT 3390; ♂ testis enlarged, November 29, 1962, MCT 3391; ♀?, November 29, 1962, MCT 3392; ♂, December 1, 1962, MCT 3393; ♂, December 2, 1962, MCT 3429; ♂, November 30, 1962, MCT 3442.

This bird was fairly common at Quoin Hill in the abaca and wild bananas and, at Kalabakan, in primary forest. Its feeding habits are the same as those of the preceding species. The order of abundance of the spiderhunters is probably best shown by the number of each species taken: *Arachnothera longirostris,* 58; *A. affinis,* 27; *A. flavigaster,* 9; *A. chrysogenys,* 4; *A. crassirostris,* 1.

Prionichilus xanthopygius (Salvadori): Yellow-rumped Flowerpecker.—*Specimens,* 7: Cocoa Research Station: ♂ testis 5 × 5 mm., 8.9 gm., August 23, 1962, MCT 2800; ♀ largest ova 3 mm., oviduct enlarged, 10.2 gm., September 13, 1962, MCT 2910; ♀ imm., 9.7 gm., September 13, 1962, MCT 2911; ♂ testis 3 × 2 mm., 9.5 gm., September 13, 1962, MCT 2912; ♀ imm., 7.0 gm., September 14, 1962, MCT 2920; ♂ testis 6 × 4 mm., vas deferens enlarged, September 26, 1962, MCT 2966; ♂, November 27, 1962, MCT 3344.

This species did not appear at Quoin Hill until August 23. The gonads of most of the adults taken from that time on appeared to be regressing from breeding condition, and several immatures were taken also, suggesting that the breeding season was over. The birds seemed to be attracted, with bulbuls, to the tree *Trema orientalis.*

Prionichilus maculatus maculatus (Temminck): Yellow-throated Flowerpecker.—*Specimen,* 1: 12 mi. N Kalabakan: ♂, October 19, 1962, MCT 3094.

I observed this flowerpecker once at Quoin Hill, in much-disturbed primary forest, but was unable to secure a specimen. Twelve miles north of Kalabakan it was found in primary forest.

Dicaeum chrysorrheum Temminck: Yellow-vented Flowerpecker.—I observed one feeding about 50 feet high among epiphytic plants in the moss forest 5.5 miles north of Tenom.

Dicaeum monticolum Sharpe: Black-sided Flowerpecker.—*Specimen*, 1: 5.5 mi. SW Tenom: ♂ testis 5 × 3 mm., December 17, 1962, MCT 3449.

I saw this flowerpecker once, in the moss forest above Tenom. Treatment of this species as monotypic follows the revision of Salomonsen (1961:17).

Dicaeum cruentatum (Linnaeus): Scarlet-backed Flowerpecker.—Along the seashore near Tawau this species fed in flowering trees. Males were pugnacious and persistently chased what appeared to be females.

Dicaeum trigonostigma dayakanum Chasen and Kloss: Orange-bellied Flowerpecker.—*Specimen*, 1: 5.5 mi. SW Tenom: ♂, December 23, 1962, MCT 3507.

This flowerpecker was found only in the moss forest above Tenom, where it was seen numerous times feeding among the epiphytic plants.

Zosterops everetti tahanensis Ogilvie-Grant: Everett's White-eye.—*Specimens*, 9: Cocoa Research Station: ♀, August 8, 1962, MCT 2734; ♂ testis 4 × 3 mm., August 8, 1962, MCT 2735; ♀, 8.6 gm., August 11, 1962, MCT 2757; ♀, 7.8 gm., August 11, 1962, MCT 2758; ♀ imm., 7.9 gm., August 11, 1962, MCT 2759; ♀, 8.2 gm., August 11, 1962, MCT 2760; ♂, 7.8 gm., August 11, 1962, MCT 2761; ♂ imm., August 11, 1962, MCT 2762; ♂ imm., 7.8 gm., August 11, 1962, MCT 2764.

At the Cocoa Research Station flocks of 20 to 40 birds were seen daily, feeding in the cocoa trees. Only once was this species seen away from the cocoa trees; this was in secondary forest where the birds were feeding in a tree about 30 feet tall. They move in flocks and are noisy.

Smythies (1960:485) states that this species occurs from the Poi Range up to the lower slopes of Kinabalu. This is apparently the first record from eastern Borneo.

Lonchura fuscans (Cassin): Dusky Munia.—*Specimens*, 11. Cocoa Research Station: ♀, July 6, 1962, MCT 2603; ♀, September 1, 1962, MCT 2847; ♂ testis 7 × 6 mm., September 1, 1962, MCT 2848; ♂ testis enlarged, September 24, 1962, MCT 2943. Tenom: ♀, January 6, 1962, MCT 3584; ♀, January 6, 1963, MCT 3585; ♂ testis enlarged, January 6, 1963, MCT 3586; ♀ several collapsed follicles, old brood patch, January 6, 1963, MCT 3587; ♀ imm., January 6, 1963, MCT 3588; ♀, January 6, 1963, MCT 3590; ♂ testis enlarged, January 6, 1963, MCT 3591.

In contrast to *L. malacca*, this species was commonly found in secondary forest away from cultivated fields. It was common at Quoin Hill and Kalabakan. On July 18, 1962, a pair was observed building a nest near Kalabakan, in a native kampong under the eave of a house. There the birds were fastening the nest to the palm thatching about 20 feet up and nearly over the door. Another pair was nesting, close to the same house, about eight feet up in a citrus tree. In Kalabakan proper, I saw a pair with fledgling young in a croton bush about six feet from the door of a house, on November 15, 1962. This nest was about seven feet up.

Lonchura malacca (Linnaeus): Chestnut Munia.—*Specimens*, 6: Tawau: ♀ imm., September 2, 1962, MCT 2862. Tenom: ♂, January 6, 1963, MCT 3589. Tuaran: ♀, January 12, 1963, MCT 3594; ♀, January 12, 1963, MCT 3595; hermaphrodite, testis 8 × 5 mm., largest ovum of ovary 2 mm., January 12, 1963, MCT 3596; ♀, January 12, 1963, MCT 3597.

This was a common bird in the lowlands away from forest. I observed it feeding on lawns in Tawau. A pair was building a nest on July 19, 1962, in an ironwood tree about 10 feet above the ground. The nest was typically bali-shaped with a side entrance. This species appears to stay in age groups when it flocks, as evidenced by the large flocks of young in first-year plumage.

The hermaphroditic specimen was of some interest, since the ovary and testis both seemed to be enlarged.

LITERATURE CITED

Amadon, D.
1956. Remarks on the starlings, Family Sturnidae. Amer. Mus. Novit., No. 1803:1-41.

Banks, E.
1950. Breeding seasons of birds in Sarawak and North Borneo. Ibis, 92:642.

Browne, F. G.
1955. Forest trees of Sarawak and Brunei and their products. Govt. Printing Office, Kuching, xviii + 369 pp., illus.

Chasen, F. N.
1935. A handlist of Malaysian birds. Bull. Raffles Mus., 11:389.
1939. The birds of the Malay Peninsula. Vol. 4. Witherby, London, xxvi + 485 pp.

Darlington, P. J.
1957. Zoogeography: geographical distribution of animals. Wiley, New York, 675 pp.

Delacour, J. and Mayr, E.
1946. Birds of the Philippines. MacMillan, New York, xv + 309 pp.

Everett, A. H.
1889. A list of the birds of the Bornean group of islands. J. Straits British Royal Asiatic Soc., 20:91-212.

Gadow, H.
1883. The catalogue of the Passeriformes, or perching birds, in the collection of the British Museum. British Mus. (Nat. Hist.), London, xiii + 385 pp., illus.

Gibson-Hill, C. A.
1950. Notes on the sea birds breeding in Malayan waters. Bull. Raffles Mus., 23:5-64.
1952. The apparent breeding season of land birds in North Borneo and Malaya. *Ibid.*, 24:270-294.

Hachisuka, M.
1953. The affinities of Pityriasis in Borneo. Proc. Seventh Pacific Sci. Conf., 4:67-69.

Lack, D.
1950. Breeding seasons in the Galapagos. Ibis, 92:268-278.

McGregor, R. C.
1910. A manual of Philippine birds. Pt. II. Govt. Printing Office, Manila, xvi + 413-769 pp.

Miller, A. H.
1963. Seasonal activity and ecology of the avifauna of an American equatorial cloud forest. Univ. California Publ. Zoöl., 66(1):1-78, illus.

Moreau, R. E.
1950. The breeding seasons of African birds. 1. Land birds. Ibis, 92:223-267.

Owen, D. F.
1963. The rufous and white forms of an Asiatic Paradise Flycatcher *Terpsiphone paradisi*. Ardea, 54:230-236.

Peters, J. L.
1934. Check-list of birds of the world. Vol. II. Mus. Comp. Zool., Cambridge, Massachusetts, xvii + 401 pp.
1940. Check-list of birds of the world. Vol. IV. Mus. Comp. Zool., Cambridge, Massachusetts, xii + 291 pp.

Peters, J. L., *et al.*
1960. Check-list of birds of the world. Vol. XV. Cambridge, Massachusetts, xii + 506 pp.
1964. Check-list of birds of the world. Vol. X. Cambridge, Massachusetts, ix + 502 pp.

Rand, A. L., and Rabor, D. S.
1959. Notes on some Philippine bulbuls. Auk, 76:102-104.

Salomonsen, F.
1961. Notes on flowerpeckers (Aves, Dicaeidae) 4. Dicaeum igniferum and its derivatives. Amer. Mus. Novit., No. 2057:1-35.

Sims, R. W.
1959. The *Ceyx erithacus* and *rufidorsus* problem. Jour. Linn. Soc. (Zoology), 296:212-221.

Smythies, B. E.
1957. An annotated checklist of the birds of Borneo. Sarawak Mus. J., 7:524-818.
1960. The birds of Borneo. Oliver and Boyd, London, xvi + 561 pp., illus.
1963. Bornean bird notes from various hands. Sarawak Mus. J., 11:269-290.

Voous, K. H.
1950a. The breeding seasons of birds in Indonesia. Ibis, 92:279-287.
1950b. On the evolutionary and distributional history of *Malacopteron*. Sarawak Mus. J., 2:300-320.
1951. Distributional and evolutionary history of the kingfisher genus Ceyx in Malaysia. Ardea, 39:182-196.

Wetmore, A.
1960. A classification for the birds of the world. Smithsonian Misc. Colls., 139(11):1-37.

Whitehead, J.
1893. Exploration of Mount Kina Balu, North Borneo. Gurney and Jackson, London, x + 317 pp.

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Natural History of Cottonmouth Moccasin, Agkistrodon piscivorus (Reptilia)

BY

RAY D. BURKETT

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INTRODUCTION

Objectives of the study here reported on were to: (1) learn as much as possible concerning the natural history and economic importance of the cottonmouth; (2) determine what factors limit its geographic distribution; (3) determine the role of the cottonmouth in its ecological community; and (4) compare the cottonmouth's life history with that of other crotalid snakes, especially the kinds that are most closely related to it.

Twenty-five live cottonmouths were kept in the laboratory for the purpose of studying behavior and fang shedding and for comparison of measurements with those of preserved specimens. Live snakes were obtained in Brazoria and Nacogdoches counties, Texas, from Hermann Park Zoo, Houston, Texas, and from the late Paul Anderson of Independence, Missouri. Preserved western cottonmouths were examined for the purpose of determining variation, distribution, food habits, body proportions, embryonic development, and reproductive cycles. The cottonmouths examined include: 221 from Texas; 33 from Arkansas; 22 from Louisiana; 2 from Illinois; and 1 each from Kansas, Mississippi, and Oklahoma.

In the preparation of this report I have examined all available literature pertaining to the cottonmouth and have drawn from these sources for comparative or additional material. Some of the more noteworthy contributions to knowledge of the cottonmouth are the general accounts of the life history by Allen and Swindell (1948), Barbour (1956), and Wright and Wright (1957); the publications by Gloyd and Conant (1943) concerning taxonomy; Klimstra (1959) concerning food habits; and Allen (1937), Parrish and Pollard (1959), Swanson (1946), and Wolff and Githens (1939b) concerning the venom. Numerous other publications, although brief, contain worthwhile contributions. Also of special interest as a source of material for comparison of cottonmouths with other crotalids are the works of Fitch (1960) on the copperhead and of Klauber (1956) on the rattlesnakes.

The cottonmouth has been well known for nearly 200 years. Wright and Wright (1957) listed the following vernacular names that are applied to the cottonmouth: black moccasin, black snake, blunt-tail moccasin, congo, copperhead, cottonmouth water moccasin, cotton-mouthed snake, gapper, highland moccasin, lowland moccasin, mangrove rattler, moccasin, North American cottonmouth snake, North American water moccasin, North American water viper, pilot, rusty moccasin, salt-water rattler, stubtail, stump

(-tail) moccasin, stump-tail viper, swamp lion, Texas Moccasin, trapjaw, Troost's moccasin, true horn snake, true water moccasin, viper, water mokeson, water pilot, water rattlesnake, and water viper.

Some of the names listed above are based upon superstition and folklore prevailing in pioneer times, and others are based upon the behavior or appearance of the snake at various ages. Names like "stump-tail moccasin" are derived from the appearance of females which have short tails or snakes that have lost part of the tail. Names like "gapper" and "trapjaw" came to be applied because of the habit of the snake's lying with its mouth open when approached. The name "cottonmouth" also was derived from this behavior, although the lining of the mouth is whitish in most other snakes. The term "rattlesnake" may have come from the fact that the cottonmouth vibrates its tail vigorously when nervous as do many other snakes, or it may have been confused with rattlesnakes. Because of the general public's fear of snakes and their reluctance to learn to discriminate between the poisonous and harmless species, numerous kinds of snakes seen in or near water have been called moccasins. The general appearance, pugnacious behavior, and whitish mouth of watersnakes (*Natrix*) have earned them a bad reputation. In fact, a great majority of the "cottonmouths" reported in many areas are found to be watersnakes.

The cottonmouth is economically important mainly because of the injurious or fatal effects of its bite and the psychological effect that its actual or suspected presence has upon many persons. The species eats a wide variety of prey items and helps to prevent overabundance of certain kinds of organisms. The venom has been used in the therapeutic treatment of blood clots owing to its anticoagulant properties (Didisheim and Lewis, 1956). It also is employed in the treatment of haemorrhagic conditions and rheumatoid arthritis, as well as in the production of antivenin (Allen and Swindell, *op cit.*:13). None of these uses of venom has become widely accepted, and its value is questionable.

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SYSTEMATIC RELATIONSHIPS AND DISTRIBUTION

Snakes of the genus *Agkistrodon* are relatively primitive members of the Crotalidae, which is one of the most specialized families of snakes. A majority of the pit-vipers are found in the Americas, but close relatives are found from extreme southeastern Europe through temperate Asia to Japan (*A. halys*) and southeastern Asia including Indonesia (*Agkistrodon* and *Trimeresurus*). Familial characters include: vertical pupil of the eye; facial pit present between the preoculars and loreal; scales usually keeled; short, rotatable maxilla bearing a large hollow fang; toothless premaxilla; chiefly hematoxic venom; and undivided anal plate.

The genus *Agkistrodon* includes about nine species in the Old World and three in North and Central America. Some of the primitive characters of the genus are: head covered with nine enlarged shields or having the internasals and prefrontals broken up into small scales; subcaudals on proximal part of tail undivided; fangs relatively short; tail lacking rattles. In one species, *A. rhodostoma*, the scales are smooth; and the female is oviparous and guards her eggs until they hatch. Other species have keeled scales and are ovoviviparous.

There is little paleontological evidence illustrating evolution of the cottonmouth or for that matter of crotalids in general. Brattstrom (1954) summarized the current knowledge of fossil pit-vipers in North America. The few fossils found of the cottonmouth are from Alacha, Brevard, Citrus, Levy, Pasco, and Pinellas counties, Florida (Brattstrom, *op. cit.*:35; Auffenberg, 1963:202). All are of late Pleistocene Age and well within the present geographic range of the cottonmouth.

Of crotalid genera only *Agkistrodon* occurs in both the Old World and the New World, suggesting that this genus is relatively old. Schmidt (1946: 149-150) mentioned several other closely related groups of animals found in both eastern Asia and eastern North America, including the reptilian genera: *Natrix*, *Opheodrys*, *Elaphe*, *Ophisaurus*, *Leiolopisma* (= *Lygosoma*), *Eumeces*, *Clemmys*, *Emmys*, and *Alligator*. Of the groups of animals now confined to these two regions the most important are the cryptobranchid salamanders, the genus *Alligator*, and the spoon-bills (*Psephurus* in China and *Polyodon* in the Mississippi drainage). Fossil evidence for these groups indicates that existing forms common to eastern Asia and eastern North America are remnants of a late Cretaceous or early Tertiary Holarctic fauna which was forced southward as the climate became gradually cooler to the north. "Other clues suggest that both *Agkistrodon* and *Trimeresurus* (*Bothrops*) moved from Asia to America, one of these presumably giving rise to the rattlesnakes." (Darlington, 1957:228).

The named, American kinds of *Agkistrodon* currently are arranged as three species: the copperhead, the cantil and the cottonmouth. The copperhead (*A. contortrix*) is divided into four subspecies, all of which are terrestrial. This species occurs from southern New England to eastern Kansas and along the Atlantic and Gulf Coastal plains, exclusive of peninsular Florida and the delta of the Mississippi River in Louisiana. It extends southwest from Kansas through the Edwards Plateau of west-central Texas. Isolated populations occur in the Chisos and Davis mountains of Trans-Pecos Texas. The cantil or Mexican moccasin (*A. bilineatus*), probably the nearest relative of the cottonmouth (*A. piscivorus*), is divisible into two subspecies and occupies a nearly complementary range from Mexico south to Nicaragua. The cottonmouth occurs throughout the coastal plains of the southeastern United States, usually at altitudes of 500 feet or less. Two subspecies are recognized, the eastern *A. p. piscivorus* and the western *A. p. leucostoma*. A revision of the genus is underway by Professor Howard K. Gloyd.

The basic pattern and various behavioral traits are common to all three species. The young are more nearly alike in appearance than adults, the copperhead and the cottonmouth being easily confused. Adults differ in color, size, body proportions, habitat, and habits. In range and habitat preference the cottonmouth more closely resembles the southern subspecies of the copperhead, *A. c. contortrix*, which is usually found in lowlands, near swamps and streams, but seldom in water.

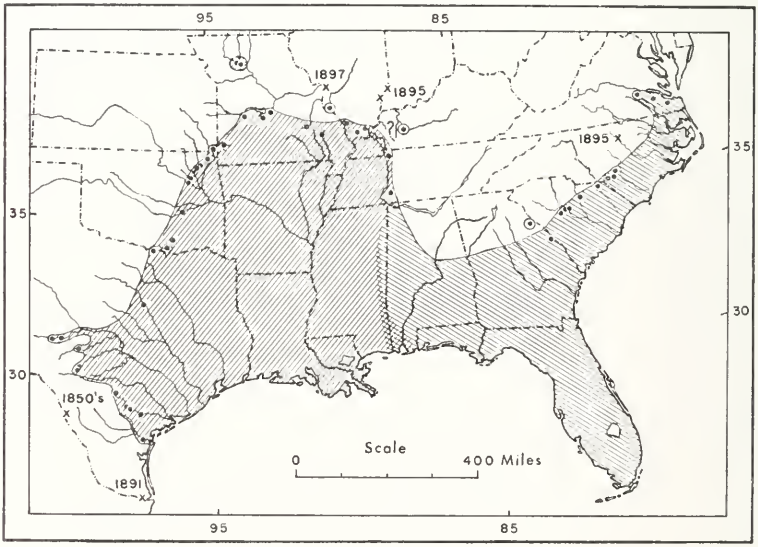

Fig. 1. Geographic range of the cottonmouth, showing marginal and near-marginal records, based largely upon maps by Gloyd and Conant (1943:165) and Conant (1958:336) but including additional records. The more important of these records (from east to west) are discussed in the following paragraphs. Crosshatching indicates the area of intergradation between the eastern and western subspecies. Old records, indicated by dates, and their sources are as follows: 1850's and 1891—U. S. National Museum numbers 4263 and 32753 respectively; 1897—Hurter (1897); and 1895—Stejneger (1895:408).

The northernmost record for the eastern subspecies is in the Petersburg area, Prince George County, Virginia (Anon., 1953:24). A sight record (Hickman, 1922:39) near Bristol, West Virginia, probably was based on a watersnake (*Natrix* sp.), since the stream in which the snake was seen flows north into the Ohio River rather than southeast through Virginia. In North Carolina the most inland record is from the Neuse River, six to eight miles east of Raleigh (Stejneger, 1895:408). Neill (1947:205) reported a population in the vicinity of Dry Fork Creek on the boundary line of Wilkes and Oglethorpe counties, Georgia. Distribution of cottonmouths in Florida is statewide, including the Keys and other offshore islands.

The ranges of the two subspecies, *piscivorus* and *leucostoma*, meet near the eastern border of Mississippi. *A. p. piscivorus* has been reported from Tishomingo County to the Gulf and east of the Loess Bluff area in central Mississippi, and *A. p. leucostoma* has been reported from this area westward. A few specimens from along the Coast indicate intergradation (Cook, 1962:33) between the two subspecies.

Barbour (1956:33) reported one specimen from Cypress Creek, in the Green River drainage, Muhlenberg County, Kentucky, and stated that suitable habitat can be found in several areas east of Kentucky Lake. Hence, cottonmouths may have entered this area via the Ohio River. Stejneger (*loc. cit.*) reported the species in the Wabash River at Mount Carmel, Wabash County, Illinois, and mentioned a former occurrence at Vincennes, Knox County, Indiana; but there are no recent records at these localities. Hurter (1897) reported having seen cottonmouths in Illinois, opposite St. Louis; Smith (1961: 265) believes that this and a population in Monroe County, Illinois, are isolated relicts, since no specimens have been found within 50 miles to the south of Monroe County. The specimens reported by Anderson (1941:178; 1945:274) near Chillicothe (three miles southwest and seven miles northwest, respectively), Livingston County, Missouri, also are thought to represent a relict population. Hall and Smith (1947:453) reported one specimen from Jasper County, Missouri, in the Spring River which flows through extreme southeastern Kansas and into Oklahoma and another in the Neosho River at Chetopa, Kansas. Both of these specimens were taken after a flood, and no additional specimens have been taken in this region. Nevertheless, sufficient habitat is probably available along the Neosho and Verdigris rivers in the southeastern part of Kansas.

In Texas the cottonmouth has penetrated marginal habitat perhaps farther than anywhere else in its range. Formerly it was thought to be limited to the country east of the Balcones Escarpment (Smith and Buechner, 1947:8), but semiarid areas of the state have been invaded primarily via the Colorado and Brazos River systems up to altitudes of 2300 feet. Two additional specimens are said to have been collected along the Rio Grande. Dr. Howard K. Gloyd (*in litt.*) stated that the specimen reported from Eagle Pass, Maverick County, is believed to have been taken in the 1850's; and the one said to have come from the mouth of the Devil's River is actually marked "near Santa Rosa, Cameron County, September 30, 1891." No additional specimens have been taken in that area; and the range now probably extends no farther south than Corpus Christi, Texas. Brown's (1903:554) knowledge of the extension of the range of the cottonmouth west of longitude 98° is probably based upon the records along the Rio Grande reported in the nineteenth century.

Three extensions of the known range in Texas are reported herein. One specimen was captured by Mr. Harry Green (HWG 346) along the San Saba River, 8.1 miles west of Menard, Menard County. The other two specimens (KU 84375 and 84376) were taken by the late Paul Anderson one and one-half miles north of Pecan Crossing, South Concho River, Tom Green County, and one mile west of Mertzon, Irion County.

In the hypsithermal period following Pleistocene glaciation, cottonmouths gradually moved northward occupying areas beyond their present range. The distributional records since the 1850's and the apparent relict populations now in existence indicate that the range of this species has since receded.

DESCRIPTION

Color and Pattern

Color predominantly brown, ranging through pale reddish-brown or dark reddish-brown, brownish-green, to almost black; 10 to 17 irregular dark brown bands on paler brown ground color; young paler (some nearly salmon pink), retaining a vivid pattern throughout first year; pattern of most individuals nearly obliterated by third year; brilliance and dullness of predominant color correlated with molting cycle (skin especially bright and shiny immediately following shedding); tip of tail yellowish in juveniles; posterior part of ventor and tail uniformly black in some adult individuals, especially females; secondary sexual differences in dorsal coloration, such as found in copperhead by Fitch (1960:102), not noted.

The eastern subspecies, *A. p. piscivorus,* has the more brilliant pattern in which the centers of the dark crossbands are invaded by the ground color. The crossbands are slightly constricted in the midline and may or may not be bilaterally symmetrical. One-half of the crossband may be displaced anteriorly or posteriorly to a slight degree or may even be completely absent. From one to several dark spots may be present within the crossbands.

The western subspecies, *A. p. leucostoma,* has a comparatively dull pattern in which the ground color does not invade the center of the crossbands. In many instances the bands are outlined by white scales, as in the Mexican moccasin (this character is not so prominent in *A. p. piscivorus* because of the paler ground color). A large, dark blotch usually occurs at the base of the crossband and may completely cross the ventral scales. The characteristic variations found in *piscivorus* are also present in *leucostoma.*

The number of bands is often difficult to count because of the dark color of some specimens. Gloyd and Conant (1943:168) reported averages of 12.5 (11 to 16) and 12.2 (10 to 16) in males and females, respectively, of *leucostoma* and ranges of 10 to 17 for males and 10 to 16 for females with averages of 13 in both sexes of *piscivorus.* On 20 specimens of *leucostoma* from Texas the average number of bands was 12.7 (11 to 15). If the number of bands differed on the two sides of an animal, the total number of the two sides was divided by two.

Scutellation

The scutellation of the cottonmouth closely resembles that of the other species of *Agkistrodon.* For example, the nine cephalic shields are characteristic of most species of *Agkistrodon,* as well as most other primitive crotalids and viperids, and most colubrids. Most individuals have an additional pair of large scales behind the parietals.

The numbers of postoculars, supralabials, and infralabials are variable. On either side the postoculars (three in most specimens) are reduced to two in some specimens. The supralabials (eight in most specimens) frequently vary (usually on one side only) from seven to nine. The number of infralabials is somewhat more variable than the number of supralabials, the usual number being 11, but 10 is also common; 8, 9, and 12 are more rare (Table 1). In 102 snakes in which these characters were examined, four different combinations of supralabials and seven combinations of infralabials were found. Both characters together yielded 16 combinations, considering only the actual number of scales and not taking into account the side of the head on which they occurred (Table 2). The combinations found in a brood of seven young from Houston, Texas, are shown in Table 3 to illustrate the variability of this character. Gloyd and Conant (1943:168) found a variation of 6 to 11 (8) and 7 to 9 (8) supralabials and 8 to 13 (11) and 8 to 12 (10.4) infralabials in samples of 301 *leucostoma* and 119 *piscivorus,* respectively (numbers in parentheses represent average). Also of interest is the variability of the scales themselves. In one instance a scale was found that had not completely divided. In another specimen the last supralabial and last infralabial were one scale that completely lined the angle of the jaw. Instances of one scale almost

TABLE 1.—Frequency of Occurrence of Various Numbers of Supralabial and Infralabial Scales in 102 Cottonmouths.

Number of scales	Specimens having number on both sides	Specimens having number on one side	Total	Percentage
		Supralabials		
7	11	24	35	25.2
8	64	27	91	65.5
9	0	3	3	2.2
		Infralabials		
8	0	2	2	1.5
9	3	10	13	9.6
10	12	32	44	32.4
11	53	22	75	55.1
12	0	2	2	1.5

TABLE 2.—Numbers of Supralabials and Infralabials of 102 Cottonmouths.

Number of individuals	Number of supralabials	Number of infralabials
37	8	11
15	8	10–11
12	7–8	11
6	7–8	10–11
5	8	10
5	8	9–10
4	7	11
3	7	9–10
3	7–8	10
2	7	9
2	7	10
2	8	10–12
2	8–9	10
2	7–8	8–9
1	7–8	9
1	8–9	10–11

crowding out another were common. In still other instances one or two supralabials were divided horizontally into two scales. Individual variation rather than geographical variation occurs in these characters.

The dorsal scales of cottonmouths are strongly keeled except that those of the two lower scale-rows on each side are weakly keeled. Also they are slightly larger than the others. Two apical pits are present on each dorsal scale. The shape of the scales and number of scale rows vary depending upon the position on the body. Scales on the neck are considerably smaller than those elsewhere on the body and are arranged in two or three more rows than those at mid-body. The skin in the region of the throat, neck, and forebody is

TABLE 3.—Variation in Numbers of Supralabials and Infralabials in a Brood of Seven Cottonmouths.

Number of individuals	Number of supralabials	Number of infralabials
1	7	9
1	7	9–10
2	7–8	8–9
1	7–8	9
1	8	9–10
1	8–9	10

TABLE 4.—Analysis of Number of Scale Rows at Three Parts of the Body in 81 Cottonmouths.

Number of scales per row	Neck		Mid-body		Anterior to anus	
	Number of individuals	Percentage	Number of individuals	Percentage	Number of individuals	Percentage
29	1	1.2				
28	3	3.7				
27	52	64.2				
26	16	18.0	2	2.5		
25	8	9.9	67	82.7		
24	1	1.2	4	4.9		
23	.....	.....	8	9.9	4	4.9
22	.....	.....	.....	.....	4	4.9
21	.....	.....	.....	.....	68	84.0
20	.....	.....	.....	.....	5	6 2

especially elastic and allows the swallowing of large prey. Posteriorly from the mid-body the scales decrease in size and become more angular, those on the tail tending to be rhomboidal and wider than long. In the region of the anus the number of scale rows diminishes rapidly, leaving only 12 to 14 rows at the base of the tail and only three rows immediately ahead of the tail tip. The tail ends in a spine composed of two scales: one scale covers the bottom, lower parts of the sides, and tip of the spine; and a shorter dorsal scale covers the top and upper parts of the sides of the basal two-thirds of the spine. The spine of embryos and young cottonmouths is blunt, but is pointed in most adults.

The number of scale rows on the neck, at mid-body, and just anterior to the anus is relatively constant at 27-25-21, respectively; but some individual variation is evident (Table 4). Since the rows are diagonally arranged, it is necessary in counting scales to proceed either anteriorly or posteriorly across the back; or the row may be counted in either direction up to the center of the back and then reversed on the other side of the snake. In order to count the scale rows in a position where no scale reduction or addition was occurring and to avoid as much error as possible, I counted from anterior to center and back on the neck, in any direction at mid-body, and from posterior to center and back near the anus. Because females generally are the larger in circumference posteriorly, they could have more scale rows than males just anterior

to the anus. The few snakes having more than 21 scale rows in the posterior region offer no conclusive evidence as to tendencies, but in both instances in which this occurred the females outnumbered the males three to one. An odd, rather than an even, number of scale rows occurs on most of the length of the snakes examined, because there is a mid-dorsal row and scale rows tend to be lost on both sides at about the same level. An example of scale reduction of one snake was as follows:

$$27\ \frac{6+7\ (13)}{5+6\ (13)}\ 25\ \frac{}{5+6\ (90)}\ 24\ \frac{6+7\ (96)}{}\ 23\ \frac{}{7+8\ (111)}\ 22\ \frac{}{7+8\ (114)}$$

$$23\ \frac{}{-6\ (118)}\ 22\ \frac{}{+6\ (119)}\ 23\ \frac{6+7\ (122)}{6+7\ (121)}\ 21\ \frac{}{+6\ (123)}\ 22\ \frac{+7,\ -5\ (125)}{}$$

$$22\ \frac{-6\ (126)}{}\ 21\ (130).$$

This scale reduction follows the method proposed by Dowling (1951b:133) in which the numbers on the midline represent the number of scale rows, upper figures refer to the right side of the snake, and figures in parentheses indicate the number of the ventral scale (counted from the anterior end of the series), thus marking the position of the addition or reduction. Addition of a row is shown by a plus sign and the number of the row, whereas reductions are shown by a minus sign and the number of the row that is lost or by a plus sign between the number of two rows that join. According to Dowling, variation in number of dorsal scales characterizes the few genera and species of snakes in which it has been studied. The time and difficulty involved in ascertaining the number of scales explain why it has not been widely used in classification.

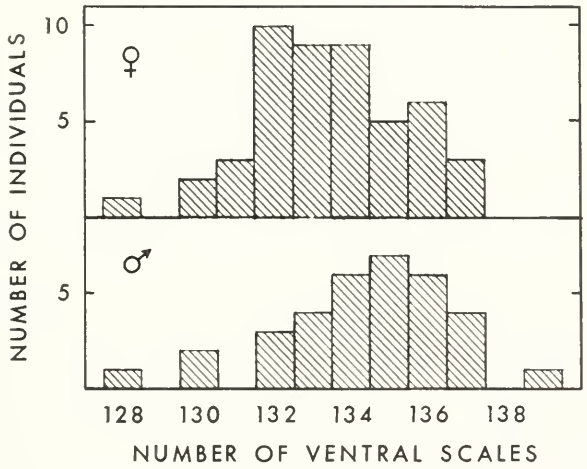

FIG. 2. Number of ventral scales in 48 female and 34 male *A. p. leucostoma*.

Ventral scales on 34 males averaged 134.4 (128 to 139), and on 48 females 133.5 (128 to 137) (Fig. 2.). Barbour (1956:34) found an average of 135.3 ventral scales on 64 males and 44 females, and Gloyd and Conant (*loc. cit.*) found an average of 134 for both males and females. The average for the eastern cottonmouth obtained by Gloyd and Conant, however, was 137 ventrals in both sexes. Some of my counts were made before I knew of the standard system of counting ventrals proposed by Dowling (1951a:97-99), in which

the first ventral plate is defined as the most anterior one bordered on both sides by the first row of dorsals. Therefore, some inconsistencies may exist in my counts. Where differences occur, Dowling's method probably will indicate the presence of an additional scale, since it appears to begin farther anteriorly on the average, than I began counting.

Analysis of caudal scales revealed sexual dimorphism. In the six specimens from Tennessee, Blanchard (1922:16) found the same thing. Caudals averaged 45.4 (41 to 50) on 34 males and 42.6 (39 to 49) on 44 females (Fig. 3). Barbour (*loc. cit.*) found an average of 45.7 (30 to 54) caudals in males and 43 (17 to 56) in females. Caudal scale counts by Gloyd and Conant (*loc. cit.*) averaged 44 (38 to 49) in males and 42 (37 to 48) in females of *leucostoma;* in *piscivorus* they averaged 48 (42 to 53) in males and 44 (41 to 49) in females. Another seldom-mentioned, unusual characteristic of the caudal

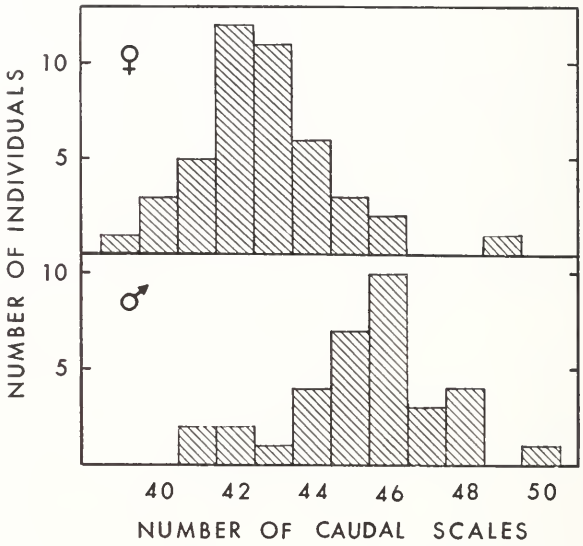

FIG. 3. Number of caudal scales in 44 female and 34 male *A. p. leucostoma.*

TABLE 5.—Caudal Scale Combinations in 95 Cottonmouths. U = Undivided; D = Divided.

Number of samples	Number of scales																
	D	U	D	U	D	U	D	U	D	U	D	U	D	U	D	U	D
25		13–35	10–32														
11	1–2	12–33	14–28														
20		16–39	1–9	1–3	3–24												
20	1–4	3–37	1–21	1–5	1–29												
4		14–30	1–8	1–7	1–8	1–4	2–10										
3	1	18–23	1–2	1–2	6–11	1–3	6–9										
4		1–17	1	1–3	1–8	1–4	1–3	1–4	13–22								
2	1–2	4–16	1	1–4	2	1	1–4	1	18–21								
1		20	1	1	1	1	6	1	3	1	11						
1		10	2	3	2	10	1	2	2	1	4	4					
1		20	1	1	2	1	1	4	4	2	4	1	3				
1	1	13	1	1	1	3	1	1	1	4	2	4	13				
1		17	1	1	2	1	1	6	2	1	2	3	2	7			
1		9	1	1	8	1	3	1	1	3	1	1	2	1	1	1	6

scales of copperheads and cottonmouths is that some are single (usually those at the base of the tail) and others divided (Table 5). To my knowledge, all other species have either single or divided scales the entire length of the tail. See Klauber (1941:73) and Fox (1948:252) concerning correlation of few scales with warm environment.

Dentition

Cottonmouths, like other pit-vipers, have their teeth reduced in number and have enlarged, highly specialized fangs. Small teeth occur on the palatine and the pterygoid in the upper jaw and on the dentary in the lower jaw. The dentary bone bears 17 curved teeth that decrease in size posteriorly. The palatine bears five small, strongly curved teeth, and the pterygoid bears 16 to 18 strongly curved teeth decreasing in size posteriorly. The numbers of teeth mentioned above in each instance refer to the number of sockets rather than the actual number of teeth, because teeth are frequently shed, leaving some of the sockets empty at any one time.

The maxillary bone has two sockets side by side which bear the poison fangs, usually one at a time. During the period shortly before a fang is to be shed, however, its replacement becomes attached in the alternate socket; and both fangs may be functional for a short time. The old fang then becomes weakened at its base, eventually breaks off, and is swallowed. At any one time four or five replacement fangs in various stages of development are found in the gum behind the functional fang. These replacement fangs, which are arranged in alternate rows, gradually enlarge as they move forward in their development and, in juveniles, are generally slightly longer than the fangs that they replace.

In 1963 I examined the fangs of 14 cottonmouths at four- to seven-day intervals for a period of six weeks. The fang-shedding cycle was found to be highly irregular, with a double condition (on one or both sides) occurring one-third of the time. Approximately the same proportion of double fangs was found in preserved individuals. A replacement period of at least five days was observed in one snake. One-half the cycle (from replacement on one side to replacement on the other) varied from five to twenty days, indicating that the cycles for each fang are independent of one another. Bogert (1943:324) found that young rattlesnakes are born with functional fangs in the two inner sockets. Nonsynchronous use of the sockets on opposite sides of the head in rattlesnakes is a later development which results from accidents or other conditions leading to a longer retention of the fang on one side than on the other (Klauber, 1956:723). I found a double set of fangs in cottonmouths only twice in the six-week period. A complete cycle was recorded in ten instances in a period of 19 to 23 days and in two instances in 32 days. One cottonmouth was examined periodically over a 34-day period by Allen and Swindell (1948:12), but a complete fang-shedding cycle was not observed. Fitch (1960:110) reported a 33-day cycle in copperheads; Klauber (1956:726) estimated the normal active life of each fang of an adult rattlesnake to be from six to ten weeks, but he made no observations to confirm his estimation.

Fangs measured from the tip of the notch of the basal lumen to the end of the fang vary from about 1.3 per cent of the snout-vent length in juveniles to about 1.0 per cent in large adults (Table 6). The fangs are longer than those of copperheads (Fitch, 1960:111). Klauber's (1956:736) figures on fang-lengths in all species of rattlesnakes are percentages of total length rather than of the snout-vent length. The fangs of various species of rattlesnakes range from nearly the same proportionate length as those of cottonmouths to some much longer.

From patterns of bites of venomous snakes, Pope and Perkins (1944:333-335) attempted to correlate number, size, and patterns of tooth marks with size and generic identity of the snake responsible for the bite. Distance between fangs is relatively constant for snakes of a particular size (Table 6) regardless of genus, but the fangs of a cottonmouth are directed outward to variable degrees, and puncture wounds could easily resemble those of a much larger snake (Table 7). Also there is no direct relationship between size of

TABLE 6.—Correlation of Relative Fang-length and Distance Between Fangs at Base with Snout-vent Length of Cottonmouths.

Snout-vent length (millimeters)	Number in sample	Average ratio of fang-length to snout-vent length (percent)	Number in sample	Average ratio of distance between fangs to snout-vent length (percent)
200–299	3	1.33	3	2.57
300–399	7	1.30	5	2.48
400–499	13	1.21	9	2.21
500–599	12	1.22	8	2.19
600–699	7	1.17	1	2.10
700–799	5	1.07	4	1.65
800–899	1	1.00	1	2.00

TABLE 7.—Contrast in Measurements Between the Base of the Fangs and Between Fang Punctures of Nine Cottonmouths (in millimeters).

Distance between base of fangs	Distance between fang punctures	Snout-vent length
7.7	13.0	400
8.7	14.0	575
10.0	22.5	526
11.0	18.0–19.0	590
12.0	18.0	793
13.0	17.0, 20.0	558, 612
15.5	23.5	800
16.0	24.0	800

snake and toxicity or amount of venom injected. Consequently information of this kind is of little or no value from a medical standpoint.

HABITAT AND LIMITING FACTORS

Although usually associated with swamps and lowlands along river bottoms, the cottonmouth lives in a variety of habitats ranging from salt marshes to cool, clear streams and from sea level to an altitude of 2300 feet. Shaded, moist areas either in or beside shallow waters are preferred, but cottonmouths occasionally wander as far as a mile from water.

In the pine-oak forests of Nacogdoches County in eastern Texas cottonmouths and copperheads are probably the most abundant species of snakes. Specimens have been collected near Nacogdoches in ponds, swamps, clear and fast-running streams with rock bottoms, and sluggish muddy streams. On the Stephen F. Austin Experimental Forest numerous cottonmouths live in a swamp until around mid-July, when it becomes dry. A small stream west of

the swamp seems to be used as a migration route to and from the swamp. Slightly more than a mile downstream cottonmouths are common in a bottomland area. The ground is always moist and no undergrowth occurs; a few small clear springs produce shallow trickles that run into a swamp. Cottonmouths can often be found here, lying in or beside the small trickles.

I have seen cottonmouths in various types of aquatic habitats in Brazoria County. In most places in this area, cottonmouths are found in association with one or more species of watersnakes (including *Natrix cyclopion*, *N. erythrogaster*, *N. rhombifera*, and *N. confluens*), which greatly outnumber the cottonmouth. Interspecific competition may be reduced somewhat by cottonmouths sometimes feeding on watersnakes.

The numerous statements in the literature concerning the habitat of the cottonmouth can be summarized most easily by the following short quotations:

Agkistrodon piscivorus piscivorus—"Marshes and lakes; ponds and streams with wooded shores; low country near water; roadside ponds; drainage ditches; coastal 'banks'; keys; some Gulf coast islands; mangrove swamps." (Wright and Wright, 1957:919.)

Agkistrodon piscivorus leucostoma—"Cypress, gum, river swamps; alluvial swamps wooded or not wooded; water courses of the south such as rivers, bayous, backwaters of small branches; hill streams in the north; . . . marshy places in prairies . . . rice fields, bottomland pools; margins of above habitats, pools, shallow lakes, swampy places, temporary flood lands. . . . In, under, or on fallen timber, in holes in banks, rocky bluffs, crayfish burrows. In short it is very aquatic." (Wright and Wright, *op. cit.*:923.)

Geographically cottonmouths differ somewhat in their ecological requirements, but are basically much alike in most respects. The areas of greatest abundance are those having 40 inches or more of annual rainfall. The northern edge of the range has a mean temperature of approximately 38° F. in January in Virginia and 30° F. in Missouri, although the lowest temperature reached in these areas is more important as a limiting factor. The annual rainfall in both Virginia and Missouri amounts to approximately 40 inches. Moisture, as well as temperature, may play an important role in the northward distribution of the species. The eastern cottonmouth seems to be less tolerant of low temperatures than the western subspecies. Mean January temperatures equal to those along the northern limits of the western cottonmouth's distribution are reached in the vicinity of Connecticut, which is north of the geographic range of the eastern subspecies.

The depths to which cottonmouths penetrate into their dens may have a limiting influence upon the geographic range, especially in the northern extremes. Bailey (1948:215) discussed the possibility that populations of snakes may be significantly depressed because of winter kill of individuals that "hibernate" at shallow depths. He speculated also that the short growing season does not allow enough time for the essentials of existence to be carried out, and the prolonged period of inactivity overtaxes the energy reserve of the species.

Available food does not seem to be of much importance as a limiting factor, for the cottonmouth is remarkably indiscriminate in its choice of prey, feeding upon almost any vertebrate animal that happens to come within reach. Competition for food, however, may play an important role.

REPRODUCTION

Courtship and Mating

A review of available literature indicates no records of courtship of the cottonmouth other than statements that breeding occurs in early spring. In a close relative, the copperhead (see Fitch, 1960:159-160), mating occurs almost any time in the season of activity but is mainly concentrated in the few weeks after spring emergence, at about the time when females are ovulating. Klauber (1956:692) concluded that along the southern border of the United States rattlesnakes normally mate in spring soon after coming out of their winter retreats; but farther north where broods are produced biennially, the mating times may be more widely dispersed, and summer and fall matings may even predominate.

The only record of copulation in the cottonmouth was reported by Allen and Swindell (1948:11), who observed a pair copulating for three hours on October 19, 1946, at the Ross Allen Reptile Institute. Davis (1936:267-268) stated that courtship in cottonmouths is violent and prolonged but did not note any nervous, jerky motions or nudging of the female along her back and sides as had been observed in other genera of snakes. Carr (1936:90) saw a male cottonmouth seize a female in his mouth and hold her, but no courtship followed.

Reproductive Cycles

Many persons have assumed that gestation periods in snakes are the intervals between mating and parturition, and that mating and ovulation occur at approximately the same time. However, retention of spermatozoa and delayed fertilization indicate that copulation is not a stimulus for ovulation.

A biennial reproductive cycle was found for the copperhead in Kansas (Fitch, 1960:162), the prairie rattler in Wyoming (Rahn, 1942:239) and in South Dakota (Klauber, 1956:688), the great basin rattler in Utah (Glissmeyer, 1951:24), and the western diamondback rattler in northwestern Texas (Tinkle, 1962:309). Klauber's (1956:687) belief that the reproductive cycle of rattlesnakes varies with climate, being biennial in the north and annual in the south, is supported by similar climatic variation in the reproductive cycle of the European viper which was discussed by Volsøe (1944:18, 149).

If data for a large number of females were arranged as are those in Table 8, they might reveal whether the breeding cycle is annual or biennial. The figures presented in Table 8 are misleading if viewed separately because of the small number of individuals included in some of the size classes.

The smallest reproductive female found measured 455 millimeters in snout-vent length. Conant (1933:43) reported that a female raised in captivity gave birth to two young at an age of two years and ten months. The size classes represented by gravid females found by Barbour (1956:38) in Kentucky indicate that breeding occurs at least by the third year.

The ovaries of female cottonmouths examined revealed ova in various stages of development. In individuals less than 300 millimeters in snout-vent length the ovaries are almost completely undeveloped; in immature individuals from 300 to 450 millimeters in length the follicles are from one to two millimeters in length; in post-partum females follicles vary in size, the largest being about seven millimeters. Reproductive females also contain follicles of various sizes.

TABLE 8.—Percentage of Gravid Females of *A. p. leucostoma* in 50 Millimeter Size Classes.

Snout-vent length	Number of gravid females	Total number in size class	Percentage gravid
450–499	3	14	21.4
500–549	7	17	41.2
550–599	8	17	47.1
600–649	5	7	71.4
650–699	2	9	22.2
700–749	2	3	66.7
750–799	1	1	100.0
850–899	1	1	100.0
Totals	29	69	42.0

One or two sets are less than three millimeters in length, and large ova that soon are to be ovulated are present. Ovarian ova found in April ranged in length from 23 to 35 millimeters. No embryonic development was observed in most individuals until June or later.

Increase in length of testes appears to be correlated with length of the individual rather than cyclic reproductive periods (Fig. 4).

The reproductive cycle in cottonmouths resembles that illustrated by Rahn (*op. cit.*:237), in which the ovarian follicles of post-partum females begin to enlarge in late summer and autumn, with ovulation occurring the following spring. By means of retaining sperm successive broods possibly are produced after only one mating. In captivity, at least, some females may not follow this biennial cycle; Stanley Roth (M. S.), biology teacher in high school at Lawrence, Kansas, had a female of *A. p. piscivorus*, from Florida, that produced broods of 14 and 12 young in two consecutive years.

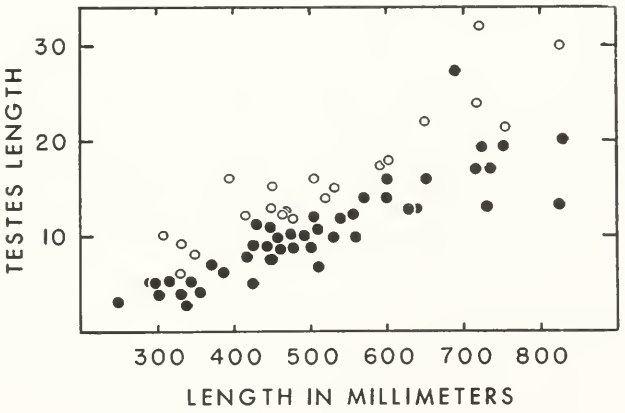

FIG. 4. Length of testes in cottonmouths of various sizes (●—left; o—right). The right testis is always longer than the left.

Embryonic Development

After ova are fertilized a three and one-half to four-month period of development begins which varies somewhat depending on the temperature. In almost every instance the ova in the right uterus outnumber those in the left. Embryos usually assume the serpentine form in the latter part of June and are coiled in a counterclockwise spiral with the head on the outside of the coil. At this time the head is relatively large and birdlike in appearance with conspicuous protruding eyes. Sex is easily noted because the hemipenes of males are everted. By late July scales are well developed and the embryo is more snakelike in appearance, but pigmentation is still absent. By mid-August the color and pattern are well developed, the egg tooth is present, the snake shows a considerable increase in size over that of the previous month, and much of the yolk has been consumed. Some females that contain well developed embryos also contain eggs that fail to develop. Sizes of ova vary irrespective of size of female and stage of embryonic development. Lengths of ova ranged from 22 to 51 millimeters in May to 35 to 49 millimeters in July and August. A two-yolked egg was found in one female.

Birth of Young

Accounts in the literature of 15 litters of cottonmouths fix the time of birth as August and September. Conant (1933:43) reported the birth of a litter in mid-July by a female that had been raised in captivity, and one female that I had kept in captivity for two months gave birth to a litter between October 19 and October 25. The conditions of captivity undoubtedly affected the time of birth in both instances.

Wharton (1960:125-126) reported the birth and behavior of a brood of seven cottonmouths in Florida. I was given notes of a similar nature by Richard S. Funk of Junction City, Kansas, on a brood of five cottonmouths. The mother of the brood was caught in June, 1962, in Tarrant County, Texas, by Richard E. Smith, and was 705 millimeters in snout-vent length. The first young was found dead in an extended position a few inches from the fetal membranes at 11:05 p. m. on August 22. The second young was born at 11:07 p. m. The intervals between the successive births were three, seven, and four minutes; and time until the sac was ruptured in each instance was six, five, eight, and 11 minutes. The time interval between the rupture of the sac and emergence of each individual was 41, 92, 154, and 34 minutes. The mother's actions in giving birth to the last four young were essentially as described by Wharton (*loc. cit.*), except that the intervals between successive births did not increase. Within one minute after rupturing the sac and while its head was protruding, each of the four living young opened its mouth widely from three to seven times, then took its first breath. Breaths for the first three hours were steady at three or four per minute but then decreased to two or three per minute. Pulse rate for the four averaged 38 per minute while at rest but increased to 44 per minute after voluntarily crawling.

Number of Young per Litter

Records of from one to 16 young per litter have been reported (Ditmars, 1945:330; Clark, 1949:259), but the average is probably between six or seven. Most accounts in the literature present information on number of ova or em-

TABLE 9.—Number of Ova Produced by Fecund Cottonmouths.

Snout-vent length in millimeters	Number in sample	Number of ova, average and extremes
450–549	10	4.1 (2 to 7)
550–649	11	4.9 (1 to 8)
650–749	4	6.3 (4 to 8)
750–849	1	5
850–949	1	14

bryos per female rather than the number of young. Size and age of the mother (Table 9) influence the number of ova produced. Allen and Swindell (1948:11) recorded three to 12 embryos in 31 cottonmouths varying in total length from 26 to 44 inches. An average of 6.5 embryos per female was found.

Mortality at birth has been recorded for almost every litter born in captivity (see Allen and Swindell, *loc. cit.;* Conant, 1933:43; Wharton, 1960:125). A female that I kept in captivity gave birth to seven young. Three never ruptured their sacs, and another died soon after leaving the sac. The effects of captivity on females may result in higher rates of deformity and mortality in young than is common in nature. Klauber (1956:699-700) estimated that the defects brought about by conditions of captivity on rattlesnakes eliminate about three young per litter.

Population Composition

No investigator has yet analyzed the composition of a population of cottonmouths according to age, sex and snout-vent length. Barbour (1956:35) did sort 167 snakes into size classes, but did not determine sex ratio, size at sexual maturity, reproductive cycles, or snout-vent length. He recorded total lengths from which snout-vent lengths cannot be computed because of differential growth rates and different bodily proportions of the two sexes. I judge from my findings that he included immature individuals in his three smallest size classes (45.5 per cent of the population). I found at least 32.5 per cent immature individuals (Fig. 5) in my material, but it was not a natural population.

The sex ratios of several small collections from natural populations varied, and no conclusions could be drawn. Females comprised 53 per cent of the specimens included in Fig. 5 and in a group of 48 embryos which represented eight broods. That percentage may not be the percentage in a natural population but is used in making assumptions because I lack better information.

Reproductive Potential

If data in Fig. 5 are representative of a natural population and if 61 per cent of the females are sexually mature, the reproductive potential can be estimated as follows: assuming a cohort of 1000 cottonmouths contains 530 females, 61 per cent of the females (323 individuals) probably are adults. If 42 per cent of these females produce 6.5 young per female in any season (Tables 8 and 9), 136 females will produce 884 young. But if 50 per cent

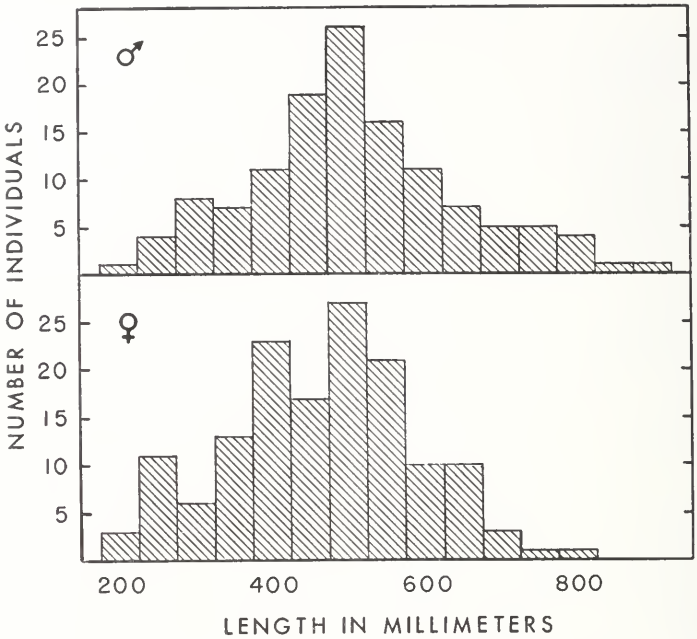

FIG. 5. Composition of a group of cottonmouths examined in this study. Individuals less than 450 millimeters in snout-vent length are considered as immature. Specimens from 200 to 249 millimeters in length are included in the 200-millimeter class, *etc.*

of the adult females are reproductive (as would be assumed if reproduction is biennial), 1050 young will be produced. Actually the number of young required per year to sustain a population is unknown, because mortality rates at any age are unknown.

GROWTH AND DEVELOPMENT

Size at Birth and Early Growth

Size at birth depends on the health of the mother. According to Fitch (1960:182), many litters of copperheads born in captivity are stunted. Seven young cottonmouths (two males and five females) born in captivity were each 185 millimeters in snout-vent length and 40 millimeters in tail length. Weights of the three living young were 10.0, 10.1, and 11.1 grams. Another litter of five young measured by Richard S. Funk were larger, and differences in the proportions of the tail length and snout-vent length suggest the sexual dimorphism found in larger individuals. However, sex of these young snakes was not recorded. Snout-vent length and tail length in millimeters were 232, 41; 243, 47; 229, 40; 240, 48; and 225, 40 in the order of their birth. These snakes are considerably smaller than the nine young of *A. p. piscivorus* reported by Wharton (1960:127) that averaged 338 millimeters total length and 28.7 grams. The yolk of one young *piscivorus* was 11.7 per cent of the total weight.

Yolk is used up in about two weeks if its rate of utilization resembles that of the copperhead as reported by Gloyd (1934:600).

Early rates of growth of three living young are shown in Table 10. On the 56th day after birth, each was fed one minnow less than two inches long. Between the 80th and 120th days three additional small minnows were fed to each snake. Young cottonmouths increase nearly 50 millimeters in length by the first spring if they inhabit warm areas and feed in autumn or winter.

Variation in size of newborn cottonmouths may be less in nature than in captivity. Average size at birth can be determined accurately by the size of young captured in early spring, at least in northern parts of the range where winter feeding and growth do not occur at all or are negligible. Total lengths of 19 juveniles thought by Barbour (1956:38) to be seven to eight months old do not differ markedly from lengths of the five newly-born young measured by Funk.

TABLE 10.—Rate of Growth of Three Young Cottonmouths.

Age in days	Snout-vent length/tail length—weight in grams		
	Female No. 1	Female No. 2	Male
2	185/40—11.1	185/40—10.1	185/40—10.0
7	192/40—	190/40—	189/40—
22	195/40—10.3	200/41.5—10.6	197/40—
80	204/40—11.7	203/42—10.4	218/48—14.3
88	.....	204/44—	.....
143	215/40.5—13.3	.....	225/48—15.1

The Umbilical Scar

The umbilical cord is broken at birth and the navel closes within a few days; but the scar, involving from two to four ventral scales, remains throughout life. Position of the scar was found by Edgren (1951:1) to be sexually dimorphic in the eastern hognose snake (*Heterodon platyrhinos*), but nothing has been published on this matter concerning the cottonmouth. Consequently, I counted the scales of several individuals from the anal plate, and there was no marked difference in the position of the scar in males and females; it varied in position from the 10th to the 18th scale. When counted from the anterior end, the scar ranged from ventral number 115 to 122 (average, 119) in 28 females and from number 117 to 126 (average, 121) in 14 males. The difference between male and female cottonmouths is not nearly so great as in *Heterodon*.

Later Growth and Bodily Proportions

The only records of growth increments in a natural population of cottonmouths are those in Table 11. The period of growth is mostly the period of activity, and differences are expected between northern and southern populations. As size increases, determination of growth rate becomes more difficult because age classes overlap in size. Growth of any individual depends not only on climate and food but also on disease and parasitism and the innate

TABLE 11.—Growth Increments in Cottonmouths (Barbour, 1956:38-39).

Number of individuals	Total length in millimeters	Estimated age in months	Estimated growth from preceding year in millimeters
19	260–298	7–8	25
11	312–337	19–20	45
40	355–485	31–32	95 ±
83	500–1000	43–44+	?

size potential. Stabler (1951:91) showed weight and length relationships in two cottonmouths for a period of six and one-half years.

My study failed to reveal any secondary sexual difference in growth rate and maximum size. Of the 306 cottonmouths measured by me, 16 males and five females exceeded 700 millimeters in snout-vent length. Two males were more than 850 millimeters long. One cottonmouth lived in captivity for 18 years and 11 months (Perkins, 1955:262). The maximum total lengths were reported by Conant (1958:186-187) to be 74 inches (1876 mm.) in *A. p. piscivorus* and 54 inches (1370 mm.) in *A. p. leucostoma.*

Proportions of various parts of the body vary considerably depending on age, size and, in some instances, sex. Heads are proportionately larger in young than in adults (Fig. 6), as is true of vertebrates in general. This larger head has survival value for the cottonmouth in permitting more venom

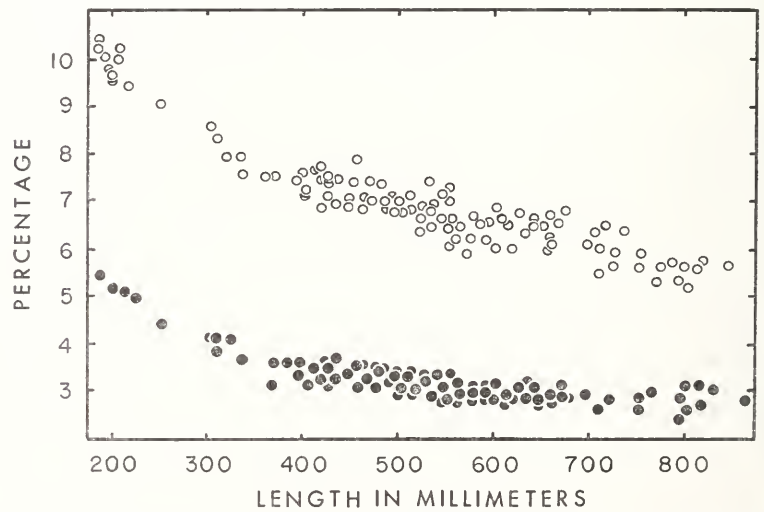

FIG. 6. Head length (o) and head width (•) expressed as a percentage of snout-vent length of living and preserved cottonmouths. Head length was measured from the tip of the snout to the posterior end of the mandible. Head width was measured across the supraocular scales, since accuracy was greater than if measured at the posterior edge of the jaw. No sexual dimorphism or geographical variation occurs in these characters.

to be produced and in permitting it to be injected deeper than would be the case if the proportions were the same as in adults. Relative to the remainder of the snake the head is considerably larger than in the copperhead (Fitch, 1960:108) and slightly larger than in the rattlesnake, *Crotalus ruber* (Klauber, 1956:152).

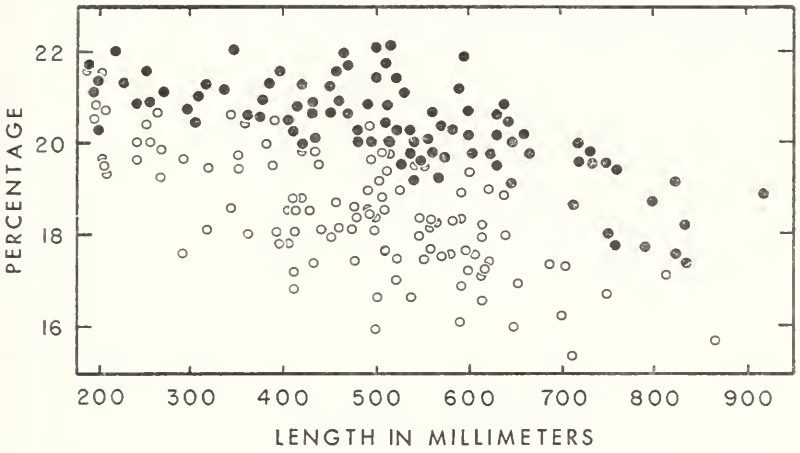

FIG. 7. Tail length expressed as a percentage of snout-vent length of living and preserved cottonmouths (●—males; o—females).

In general, tails are relatively longer in males than in females of the same size (Fig. 7), except that there is little or no difference at birth. Growth of the tail in males proceeds at a more rapid rate. In certain individuals sex cannot be recognized from length of the tail relative to snout-vent length because overlapping occurs, especially in medium-sized individuals. Similar changes of proportions with increase in age occur in copperheads (Fitch, 1960: 106) and rattlesnakes (Klauber, 1956:158-159), but the tail of the cottonmouth is relatively much longer.

SHEDDING

The Shedding Operation

Shedding of the skin is necessary to provide for growth and wear in snakes. The milkiness or bluing of the eyes, which causes partial blindness, marks the initial stage of shedding and is caused by a discharge of the exuvial glands that loosens the old *stratum corneum* from the layer below. In four to seven days the opaqueness disappears, and the snake sheds after an additional three to six days (Table 12). Young snakes first shed within a few days after birth and generally shed more frequently than adults, but the interval is variable. The eyes of three young cottonmouths observed by Wharton (1960:126) became milky on the fourth day but cleared on the seventh day, and the skin was shed on the eighth day. The eyes of three young kept by me became milky two to three days after birth, cleared on the seventh to tenth days, and the skin was shed on the thirteenth day. Possibly the relatively long interval in

TABLE 12.—Duration of Preparatory Period (in days) to Shedding in 11 Cottonmouths.

Duration of cloudiness of eyes	Time between clearing and shedding	Time from beginning of cloudiness until shedding
5	6	11
7	3	10
–	–	6
–	–	6
5	3	8
4	6	10
7	3	10
5	6	11
5	3	8
7	–	–
7	3	10
$\overline{\times}$ 5.4	$\overline{\times}$ 3.8	$\overline{\times}$ 9.0

this instance resulted from low relative humidity in the room where the snakes were kept. According to Fitch (1960:134), litters of young copperheads usually shed within three to ten days after birth; but under unusually dry conditions shedding did not occur for several weeks.

Cottonmouths as well as other snakes usually do not feed until after the skin is shed and are generally quiescent during the period preceding shedding, except that immediately before shedding they become active and rub their snouts on some rough object and may yawn several times seemingly in an attempt to loosen the skin along the edges of the lips. After the skin is loosened from the head, more rubbing against rough surfaces and writhing serves to pull the old skin off, turning it inside out. Once the old skin has passed over the thick mid-body, the snake often crawls forward using rectilinear locomotion until the skin is completely shed. It normally comes off in one piece; but, if the snake is unhealthy or has not had sufficient food or water, the skin may come off in patches. Frequently one or both of the lens coverings are not shed immediately and impair the sight. Bathing or swimming ordinarily causes dried skin to peel off; and, because of the cottonmouth's aquatic habits, its chances of shedding successfully are much greater than those of less aquatic snakes. Cottonmouths that have recently shed have bright and glossy patterns, in contrast to the dull and dark appearance of those that are preparing to shed.

Frequency of Shedding

Most of our knowledge concerning the frequency of shedding is based upon observations of captives. It is known that the intervals between exuviations are largely dependent upon the amount of food taken and the rate of growth. Unless laboratory conditions closely resemble those in the field, shedding frequencies in captives probably differ much from those of free-living snakes.

Only two of my captives shed twice. The intervals between exuviations

in the two snakes were eight and five months, lasting from August to April and from December to May, respectively. Ten other snakes shed once in the period from January through July. Stabler (1951:91) presented data concerning shedding of two cottonmouths kept 12 and 14 years in captivity. One shed 25 times in 12 years and the other shed 37 times in 14 years, giving an average of 2.1 and 2.6 per year, respectively. Neither of the snakes shed from December through March, but the period of shedding corresponded to the period of greatest activity and growth. In Florida, cottonmouths shed four to six times a year, according to rate of growth (Allen and Swindell, 1948:7).

FOOD HABITS

Methods of Obtaining Prey

Food is obtained by a variety of methods depending on the type of food, age of the cottonmouth, and possibly other factors. Some captives lie in ambush and others crawl slowly in active search. At the first cue of possible prey, either by sight, scent, or differential temperature detection by the pit, the snake appears to become alert and flicks its tongue out at fairly rapid intervals.

By means of the facial or loreal pit found in all crotalids, the snake is able to detect objects having temperatures different from that of the surroundings of the objects. In detecting prey the tongue acts to sharpen the sense of "smell" by conveying particles to Jacobson's organs in the roof of the mouth. On many occasions cottonmouths appeared to rely solely on sight; they passed within a few inches of prey, apparently unaware of its presence until it moved. When pools of water begin to dry up toward the end of summer, cottonmouths often congregate and feed on dying fish. In these instances the fish are usually taken as they come to the surface. In laboratory observations moccasins seize live fish and some moccasins carry the fish until they have received lethal doses of venom; afterward the fish are swallowed. But grasping and manipulation of the prey occurs without the fangs' being employed, especially in the case of dead fish. On one occasion a cottonmouth was observed to grasp the edge of a glass dish that had contained fish and apparently retained the odor. On another occasion I placed several fish in a bowl, rubbed a stick on the fish, and then touched each snake lightly on the nose with the stick. The snakes crawled directly to the bowl and began feeding. At other times these same snakes crawled around the cage in an apparent attempt to locate the food but paid little attention to fish held in front of them. If the catching of prey under natural conditions were as uncoordinated as it sometimes is in captivity, the snakes probably would not be able to survive.

Wharton (1960:127-129) described tail-luring in one individual of a 76-day-old brood of cottonmouths. The snake lay loosely coiled with the tail held about six centimeters from the ground; a constant waving motion passed posteriorly through the terminal inch of the tail. These movements ceased at 7:20 p. m. but were resumed at 7:40 a. m. the following day. All observations were under artificial light. The "caudal lure" as a means of obtaining prey has been described in other species and related genera by Neill (1960:194) and Ditmars (1915:424).

Various authors have suggested that the method of capture differs according to the kind of prey. Allen and Swindell (1948:5) stated that cottonmouths retain their hold after striking fish or frogs but will release a mouse after delivering a bite and are timid in striking at larger rodents. Neill (1947:203) noted that a cottonmouth always waited several minutes after biting a large rat before approaching its prey. This same type of behavior has been reported for copperheads (Fitch, 1960:194) and rattlesnakes (Klauber, 1956:618).

Cottonmouths observed by me retained a strong hold on fish, frogs, and sometimes mice, but almost always released large mice and baby chicks, which were not eaten until after death.

Different behavior according to type of prey is correlated with ability of prey to retaliate, although some animals may not be released because they could easily escape. For instance, a frog could hop far enough to escape in a matter of seconds if released. A 73-millimeter *Rana pipiens* that I observed was bitten twice within one and a quarter hours and died 45 minutes after the last bite. Its movement was uncoordinated by the time of the second bite, but it could have escaped had the frog not been confined. Although it is doubtful that normal, healthy fish are frequently captured by cottonmouths, Allen (1932:17) reported that a cottonmouth was seen pushing a small, dead pike about on the surface of a stream. A wound on the belly of the fish indicated that it had been bitten. A 17-gram creek chub (*Semotilus*) and a 13.7-gram bass (*Micropterus*) were injected by me with one-fourth cubic centimeter of fresh venom near the base of the tail in order to determine whether the fish could escape after being bitten and released. The creek chub flipped onto its back after a minute and 45 seconds and gill movements stopped in eight minutes and 35 seconds; the bass flipped over after 50 seconds and died in two minutes and 10 seconds. The venom immediately affected both fish, and it is unlikely that either could have swum more than a few feet.

After its prey has been killed, a cottonmouth examines the body from end to end by touching it with the tongue. Then the animal is grasped in the mouth without the use of the fangs and is slowly manipulated until one end (usually the head) is held in the mouth. The lengthy process of swallowing then takes place, the fangs and lower jaws alternately pushing the prey down the throat.

Food and Food Preferences

The cottonmouth seems to be an opportunistic omni-carnivore, because it eats almost any type of flesh that is available, including carrion. It feeds primarily upon vertebrates found in or near water; but invertebrates and eggs have also been found in the diet. The only potential prey items that seem not to be normally eaten are bufonid toads and tadpoles. I have occasionally offered tadpoles and frogs to cottonmouths, but only the frogs were accepted. But, Stanley Roth kept a cottonmouth in captivity that ate both toads and tadpoles. If tadpoles are commonly eaten, their probable rapid digestion would make identification almost impossible.

Following is a list of known foods of the cottonmouth:

Captivity: ". . . rattlesnake. . . . The same moccasin also killed and ate a smaller snake of its own species. . . ." (Conant, 1934:382.)

Florida: "3 heron feathers, bird bone, *Eumeces inexpectatus*, 3 fish all under one inch in length, 1 heron egg shell" (Carr, 1936:89). According to Allen and Swindell (1948:5), "the food included other moccasins, prairie rattlesnakes, kingsnakes, black snakes, water snakes, garter snakes, ribbon snakes, and horn snakes . . . most of the species of frogs, baby alligators, mice, rats, guinea pigs, young rabbits, birds, bats, squirrels, and lizards. . . . a mud turtle. . . . a case of a four footer eating ten to twelve chicken eggs. The most common food appears to be fish and frogs. Catfish are included on this list. . . ." Yerger (1953:115) mentions "an adult yellow bullhead, *Ameiurus natalis* . . . 306 mm. in standard length [from a 63-inch cottonmouth]."

Georgia: ". . . full grown *Rana catesbeiana,* several foot-long pickerel. . . . dead fish if placed in a pan of water. . . . *Natrix sipedon fasciata* and *Masticophis flagellum.* . . . rats. . . . Toads and large *Eumeces laticeps* were always ignored." (Neill, 1947:203.) "*Natrix, Heterodon, Kinosternon, Rana, Hyla cinerea, Microhyla,* Microtine [*Pitymys pinetorum*]." (Hamilton and Pollack, 1955:3.)

Mississippi: ". . . *Hyla gratiosa.* . . . In captivity specimens have eaten frogs, mice, birds, dead fish, pigmy rattlers and copperheads. Toads . . . were refused" (Allen, 1932:17). One moccasin "disgorged a smaller decapitated moccasin . . . killed the day before by boys" (Smith and List, 1955:123).

Tennessee: "Beetles in one stomach; lizard (*Eumeces*) in another stomach; small snake (*Natrix*) in one intestine, and hair in another intestine. One stomach contained numerous bits of wood, up to four inches in length. . . ." (Goodman, 1958:149.)

Kentucky: "*Siren intermedia* was the most abundant food item in both volume and occurrence. Frogs of the genus *Rana* ranked second. Together, these two items comprised almost ⅔ of the food of the snakes. The other food items were distributed among the fishes, reptiles, and other amphibians [one *Rana* tadpole included]." (Based on 42 samples—Barbour, 1956:37.)

Illinois: (Based on 84 samples—Klimstra, 1959:5.)

Food Item	*Per cent Frequency of Occurrence*	*Per cent Volume*
Pisces	39.3	31.9
Amphibia	36.9	26.0
Reptilia	25.0	18.2
Mammalia	30.9	17.9
Gastropoda	17.8	1.0
Miscellaneous (Algae, Arachnida, Aves, Insecta)	25.0	5.0

Louisiana: Penn (1943:59) mentions that a "female had just eaten two young cottonmouths. . . ." Clark (1949:259) mentions "100 specimens—34 fish; 25 *Rana pipiens;* 16 *Rana clamitans;* 7 *Acris;* 4 *Natrix sipedon confluens;* 8 birds; 5 squirrels. . . . catfish thirteen and one-half inches in length . . . smallmouth black bass [eleven inches]."

Oklahoma: Force (1930:37) remarks that the moccasin "eats bullfrogs . . . but refuses leopard frogs." Trowbridge (1937:299) writes: "several sun perch. . . . Another had eaten six catfish six to ten inches long. . . . a water snake (*Natrix s. transversa*) about 18 inches long. . . . frogs, mostly *Rana sphenocephala.*" Carpenter (1958:115) mentions "a juvenile woodthrush. . . . Seven last instar cicadas. . . . a young cottontail." According to Laughlin (1959:84), one moccasin "contained the following items: 18 contour feathers of a duck, probably a teal; one juvenile cooter turtle, *Pseudemys floridana;* and a large mass of odd-looking unidentifiable material. The other cottonmouth contained one juvenile pond turtle, *Pseudemys scripta.* . . ."

Texas: ". . . several . . . feeding on frogs. . . . One . . . found DOR was found to contain a large catfish." (Guidry, 1953:54.)

Of 246 cottonmouths that I examined for food items, only 46 contained prey in their digestive tracts. Almost all of the snakes examined were museum specimens that had been collected at many places over a period of about 40 years. It was not known how long each had been kept alive before being preserved. Therefore it was impossible to determine what proportion of any population of cottonmouths could be expected to contain food. The food items were not analyzed numerically because the scales and hair, by means of which many food items in the intestine were identified, yielded no clue as to the number of individuals actually present unless several

distinct kinds were found. Each occurrence of scales or hair was thus recorded as a single individual, although some such occurrences may have represented more than one animal. The contents of some stomachs were so well digested that it was difficult to determine the number of items present. As a rule only one food item was present in a digestive tract, but a few tracts contained several items of the same or different species. Three frogs (*Acris crepitans*) were in one snake and three hylas (*Hyla versicolor*) in another. Still another individual captured beside a drying pond contained six individuals of *Lepomis* each about three inches long and two pikes (*Esox*) about six inches long.

The "unidentified" category (Table 13) refers to jellylike masses in the stomach or material in the intestine in which no scales, feathers, hair, or bones

TABLE 13.—Analysis of Food Items of 46 Cottonmouths Collected in Arkansas, Louisiana, and Texas (1922-1962).

FOOD ITEMS	Number of samples in which item occurred	Percent frequency of occurrence	Estimated weight in grams	Estimated percentage by bulk
Fish	(7)	13.2		18.4
Esox sp.	1		20	
Lepomis sp.	2		15	
Unidentified	4			
Amphibians	(12)	23.0		20.4
Scaphiopus hurteri	1		13	
Acris crepitans	2		4	
Hyla cinerea	2		12	
Hyla versicolor	1		12	
Rana catesbeiana	1		20	
Rana pipiens	3		15	
Unidentified	2			
Reptiles	(15)	28.4		29.9
Pseudemys scripta	2		15	
Anolis carolinensis	1		6	
Eumeces fasciatus	1		7	
Lygosoma laterale	2		5	
Natrix sp.	1		10	
Natrix erythrogaster	2		10	
Agkistrodon piscivorus	2		20	
Crotalus sp.	1		30	
Unidentified snakes	3			
Birds	(4)	7.6		18.6
Anhinga anhinga (juv.)	1		60	
Egret (head and neck)	1		20	
Passeriformes	2		20	
Mammals	(6)	11.3		12.7
Blarina brevicauda	1		12	
Cricetinae	5		18	
Unidentified	(9)	17.0		

could be found. Most of the unidentifiable matter could be assumed to consist of remains of amphibians, since they leave no hard parts. If this assumption is correct, amphibians comprise about 40 per cent of the diet. Since intestinal contents were included, a volumetric analysis was not feasible. Therefore, the weight of each type of food item was estimated and the percentage by bulk calculated from it (Table 13).

Pieces of dead leaves and small sticks constituted most of the plant material found and presumably were ingested secondarily because they adhered to the moist skin of the prey, especially to fish and amphibians. However, some plant materials probably are eaten because they have acquired the odor of the prey. One cottonmouth contained a *Hyla cinerea*, several leaves, and five sticks from 37 to 95 millimeters long and from 12 to 14 millimeters in diameter.

Most reports in the literature state that gravid females do not feed, but four gravid females examined by me containing large, well-developed embryos also contained evidences of having recently fed. Two of them had scales of snakes in the stomach or intestine, one contained a six-inch *Lepomis*, and the other had hair in the intestine and the head and neck of an adult egret in the stomach.

MORTALITY FACTORS

Natural Enemies and Predators

Published records of other animals preying on cottonmouths or killing them are few. Reptiles more often than other classes of vertebrates prey on the cottonmouth. McIlhenny (1935:44) reported on the scarcity of snakes in areas where alligators were present. Predation on cottonmouths by indigo snakes (*Drymarchon corais*) was reported by Conant (1958:153) and Lee (1964:32). Allen and Swindell (1948:6) obtained a photograph of a kingsnake (*Lampropeltis getulus*) killing a cottonmouth but thought that moccasins are not eaten by *L. getulus*. However, one occasion reported herein shows that cottonmouths are eaten by kingsnakes; and Clark (1949:252) reported finding 13 cottonmouths, along with other prey, in the stomach contents of 301 kingsnakes (*L. g. holbrooki*) from northwestern Louisiana. Cannibalism is also common among cottonmouths. Klauber (1956:1058;1079) cited predation on cottonmouths by a blue heron (*Ardea herodias*) and a largemouth bass (*Micropterus salmoides*). Man is probably the greatest enemy of the cottonmouth. Intentional killing, capturing, road kills, and alteration of the environment destroy large numbers.

Parasites and Diseases

Allen and Swindell (1948:12) listed several diseases and parasites of snakes and stated that "some moccasins captured in the woods are so poor and weak from parasitic infection that they can barely crawl." The only kind of ectoparasite found on captive cottonmouths in the course of my study was a snake mite, *Ophionyssus natricus*. An infestation of that mite was thought to be partly responsible for the death of one captive moccasin. Other moccasins spent increasing amounts of time in their water dish after they became infected with mites. Under natural conditions frequent swimming probably keeps cottonmouths nearly free of mites.

Endoparasites found included lung flukes, stomach nematodes, and tapeworms. Lung flukes (*Ochetosoma* sp.) were found in 16 of 20 captive cotton-

mouths. Snails and frogs serve as intermediate hosts for various stages in the life cycle of these flukes. The high percentage of cottonmouths infested with flukes is indicative of the use of frogs as a major source of food. Less than ten flukes were usually observed in the snakes' mouths but occasionally more were seen. One snake was observed thrashing about in its cage for nearly an hour, after which time it died. Upon examination of the mouth, 32 flukes were found, most of which were located in the Jacobson's organs. Whether or not flukes caused the death is not known. Nematodes (*Kalicephalus* sp.) were found in the stomach of each of several preserved specimens; most of these snakes had no food in their digestive tracts. In a high percentage of the moccasins, tapeworms (*Ophiotaenia* sp.) were in the duodenum, in many instances so tightly packed as seemingly to prevent passage of food. The importance of fish in the diet is reflected by the high percentage of snakes containing tapeworms. An unidentified cyst (?) about an inch long and containing two hooks on one end was found attached to the outer wall of the stomach of a cottonmouth. Yamaguti (1958) listed all the kinds of helminths known from cottonmouths.

Miscellaneous Causes of Death

Munro (1949:71-72) reported on the lethal effect of 10 per cent DDT powder on two young cottonmouths which were dusted with it to kill mites. Herald (1949:117) reported an equal effect caused by spraying a five per cent DDT solution in a room with several snakes. All but three large cottonmouths, which were under shelter at the time of spraying, were killed.

One individual that refused to eat was dissected soon after death, and a short piece of a branch on which two large thorns were located at 90° angles was found blocking the intestine at the posterior end of the stomach.

An unexpected and probably unusual circumstance caused the death of two captives. After cleaning a cage containing five cottonmouths and placing several mice in the cage for food, I noticed two of the snakes lying stretched out, partially on one side, and almost unable to move. At first I thought they had been bitten by other snakes which were in pursuit of the mice. The two died after two days. When a similar incident occurred in another cage, I removed the "bitten" snake and it fully recovered after 11 days. When the same symptoms were observed in a garter snake in another cage, I realized that in each instance the cage had been cleaned and fresh cedar chips placed in it immediately prior to observation of these symptoms. Fine cedar dust on the chips had evidently poisoned the snakes.

BEHAVIOR

Annual and Diel Cycles of Activity

In the days following emergence in spring, cottonmouths often endure uncomfortable and even dangerous temperatures in order to obtain food and mates. They are more sluggish at this time and more vulnerable to predation than later in the season when temperatures are optimal. Fitch (1956:463) found that copperheads in northeastern Kansas begin their annual cycle of activity in the latter part of April, when the daily maximum temperature is about 22° C. and the minimum is about 4° C., and become dormant in late

October or early November, at which time the daily maximum temperature is about 15° and the minimum is about 0°. Indications are that in the northern part of its range the annual activity cycle of the cottonmouth resembles that of the copperhead in northeastern Kansas. Klimstra (1959:2) captured cottonmouths from April to October in southern Illinois. Barbour (1956:36) collected large numbers of them in early April in Kentucky and stated that they migrate from swamps to wooded hillsides in late August and early September. Spring migrations begin after a few consecutive warm days in March. In northern Oklahoma cottonmouths have been found along the Verdigris River as early as March, suggesting that a few winter in crayfish holes and mammal burrows. The majority of individuals found in this area were at denning sites along cliffs above the river and emerged later than those near the river (Dundee and Burger, 1948:1-2). In Virginia cottonmouths have been seen as early as March 5 (Martin and Wood, 1955:237) and as late as December 4. They have been observed in migration from the swamps of the barrier beach to the mainland in late October and early November in southeastern Virginia (Wood, 1954a:159). According to Neill (1947:204), the cottonmouth tolerates lower temperatures than do most snakes in Georgia and is one of the last to go into hibernation. Allen and Swindell (1948:4) stated that cottonmouths usually bask during the mornings of the cooler months in Florida, but they mentioned nothing of denning such as occurs farther north. Although winter aggregations occur in the northern parts of the range, I have never seen such aggregations in the South. However, in one instance related to me by a reliable observer, seven cottonmouths were found together on a creek bank near the Gulf Coast in early spring.

During late summer and early autumn, fat is deposited in lobes in the lower abdomen in preparation for the period of winter quiescence. Gravid females usually do not feed so frequently or so much as other snakes, because they tend to become inactive as the ova develop. Whether or not females feed heavily after parturition and previous to denning is not known. Peaks of activity in autumn may be caused by final attempts to feed before denning and by the appearance of large numbers of newborn young. The young usually have from one to two months in which to feed before the advent of cold weather. According to Barbour's (*op cit.*:38) findings, the young probably feed before hibernation because they grow substantially in winter. For those that do not feed, the rate of survival is perhaps much lower.

In preparation for winter, cottonmouths migrate inland, usually to dry forested hillsides where they den, commonly among rocks at the tops of bluffs, along with several other species of snakes. In such aggregations there is no hostility and each individual may derive benefit from contact with others by which favorable conditions of temperature and humidity are maintained.

Neill (1947:204) has found many specimens in winter by tearing bark from rotting pine stumps on hillsides overlooking lakes or streams. On cold days they evidently retreat below the surface, while on warm days they lie just below the bark or emerge and bask. Neill believes that the use of stumps by cottonmouths is an innate pattern of behavior, because of the large number of young-of-the-year found in such surroundings. Cottonmouths were observed in winter also under logs and stumps by Allen (1932:17). I have twice observed cottonmouths crawling into crayfish burrows along the Gulf Coast of Texas, and suppose they are used as denning sites to some extent.

The diel cycle of activity of cottonmouths is of necessity closely related to the seasonal cycle. Since optimal temperatures determine activity, the diel cycle varies greatly from time to time. It has been well established that cottonmouths, like most other crotalids and many snakes of other families, prefer nocturnal to diurnal activity, even though the temperature may be less favorable at night. This preference is correlated with increased nocturnal activity of frogs and reptiles that constitute the principal food supply.

During spring and autumn, activity is more restricted to the day and long periods of basking occur. However, as hot weather approaches, basking occurs mainly in the morning and evening and activity becomes primarily nocturnal. But, in well shaded, moist forests, cottonmouths feed actively in the daytime.

Availability of food also has an important influence upon activity. Allen and Swindell (*op. cit.*:5) stated that moccasins congregate around drying ponds and feed on dying fish until the moccasins can hold no more. They then usually stay nearby as long as food remains. In an area of the Stephen F. Austin Experimental Forest near Nacogdoches, Texas, many cottonmouths journey daily to and from a swamp and a dry field, evidently to feed on rodents inhabiting the area. Ten individuals captured along a snake-proof fence that was built 30 yards from the swamp were found lying coiled along the fence after 4:30 p. m., at which time the area was shaded. On another occasion, I captured a large cottonmouth that was feeding upon dying fish in a drying pool about 10:30 a. m. on August 19, 1962.

Because of the aquatic habits of the cottonmouth, relative humidity probably has little influence on the snake's activity. However, cottonmouths are more restricted to the vicinity of water in dry weather than during rains or muggy weather when many of their natural prey species also move about more freely. Increased activity on cloudy days may result from protection from long exposure to sunshine. Torrential rains and floods, such as those following hurricanes along the Gulf and Atlantic coasts of the southeastern United States, bring out quantities of snakes of all species. Rattlesnakes and cottonmouths in particular are killed by the thousands at these times because they seek shelter in human habitations. However, these are unusual circumstances and do not reflect voluntary activity as a result of preferences.

Thermal reactions of reptiles were classified by Cowles and Bogert (1944) into several categories. For each species there is a basking and normal activity range limited by the voluntary minimum and voluntary maximum at which the animal seeks shelter. Beyond this normal range are the critical thermal minimum and critical thermal maximum (C. T. M.) at which effective locomotion is prevented. The lethal minimum and maximum are those temperatures at which short exposure produces irreparable damage, and death inevitably results. These classifications are modified somewhat by seasonal or laboratory acclimation or by the physiological state of the animal. The C. T. M. of five cottonmouths was determined by placing each individual in an enclosed area and heating it with an infrared lamp. Cloacal temperatures were taken with a Schultheis quick-recording thermometer as soon as the snake could no longer right itself when placed on its back. All temperatures were in degrees Celcius. The C. T. M. averaged 39.2° (38.0° to 40.0°). A temperature of 38.0° was lethal to one individual. These cottonmouths had

been in captivity for nine months. The behavior of the snakes during heating resembled those instances described by Klauber (1956:382-387) for rattlesnakes. As the body temperature of the snakes rose past the optimum, each individual became disturbed and tried to escape from the enclosure. The snakes soon became frantic in their efforts to escape. After about five minutes the mouth was opened and heavy, slow breathing was begun, accompanied by a loss of coordination and a slowing down of movements. The snakes writhed spasmodically for a few seconds and then lay still, usually with the mouth open. Recovery was begun by rolling on the belly and flicking the tongue, followed by movements of the head and then the body. Cottonmouths are rarely exposed to dangerously high temperatures owing to their semi-aquatic habits, but there are probably occasions when individuals reach the C. T. M. for the species.

Basking

Since activity, digestion, and gestation depend upon adequate internal temperatures, there must be a process by which these temperatures are attained and for an appropriate time maintained. Basking is important in this respect. The cottonmouths prefer to lie in a coiled position and, during basking, can usually be found beside bodies of water or on branches of dead trees overhanging the water. They are good climbers and have a prehensile tail that is frequently employed in descending from small branches. Since cottonmouths are semi-aquatic and are often exposed to temperatures that are lower than those of the air, they either must bask more often than terrestrial snakes or tolerate lower temperatures. Length of the period of basking is determined not only by amounts of insolation and temperature but also by the size of the snake. A smaller snake can reach its optimum temperature more rapidly because of a higher surface-to-volume ratio. Another factor that may play a minor role in the rate of temperature change is the color of the snake. The wide variation in color of cottonmouths probably affects rates of heat increase and loss due to direct radiation. Slight hormonal control of melanophores described in snakes by Neill and Allen (1955) also may exert some influence on the length of time spent basking. No rates of temperature increase or decrease are available for cottonmouths.

Coiling

While inactive the cottonmouth spends most of its time lying in a coiled position with the tail outermost, with the body usually wound into about one and one-half cycles, and the head and neck in a reversed direction forming a U- or S-shaped loop. From this position the snake is able to make a short strike or a hasty getaway if necessary. In my opinion this position is used primarily for basking or resting and only secondarily for feeding. Most individuals appear to pursue their prey actively, not lying in ambush for the approaching prey to the extent that most other crotalids do.

Many of the cottonmouths that I kept in captivity were observed in a coiled position for periods up to three or four days. Under natural conditions, however, they are more active. Young cottonmouths are inclined to remain in a coiled position for longer periods than older individuals.

Locomotion

Four distinct types of locomotion have been described in snakes: horizontal undulatory, rectilinear, sidewinding, and concertina (Klauber, 1956: 331-350). Most snakes are capable of employing two or more of these types of progression, at least to a certain degree; but horizontal undulatory locomotion is the most common method used by the majority of snakes, including the cottonmouth. In this method the snake's body is thrown into lateral undulations that conform with irregularities in the substrate. Pressure is exerted on the outside and posterior surface of each curve, thus forcing the body forward.

Rectilinear locomotion is more useful to large, thick-bodied snakes which use this method of progression, chiefly when they are prowling and unhurried. This method depends upon the movement of alternate sections of the venter forward and drawing the body over the ventral scales resting on the substratum by means of muscular action. This mode of locomotion was most frequently observed in captive cottonmouths when they were crawling along the edge of their cages, especially when they were first introduced to the cages and toward the end of the shedding process. The other two types of locomotion, sidewinding and concertina, have not, to my knowledge, been observed in the cottonmouth.

Both the cottonmouth and the cantil have definite affinities for water and are as likely to be found in water as out of it. Copperheads and rattlesnakes, although not aquatic, are good swimmers. When swimming, a motion resembling horizontal undulatory progression is used.

Disposition

The number of different opinions expressed in the literature concerning the cottonmouth's disposition is not at all surprising. As with any species there is a wide range of individual temperament, which is affected by many factors. The cottonmouth is considered by some writers to be docile while others consider it to be highly dangerous. Allen and Swindell (1948:7) described the variability in temperament, even among individuals. They wrote: "On rare occasions, moccasins are found which will attack. A perfectly docile snake will turn and bite viciously without any apparent reason." They also recounted a case in which a cottonmouth was kept as a pet for six years, being allowed the freedom of the house. Smith and List (1955:123) found them ". . . surprisingly docile in the gulf region [Mississippi], displaying none of the pugnacity of more northern cottonmouths." Smith (1956:310) stated: "Unlike the copperhead, cottonmouths are pugnacious; their powerful jaws, long fangs, vicious disposition and potent venom make them a very dangerous animal."

My own observations are in general agreement with the statements of Allen and Swindell (*loc. cit.*). In my encounters with cottonmouths, I have never found any aggressive individuals except for three juveniles that were born in captivity. In their first three days in the laboratory these juveniles were observed to strike repeatedly whenever anyone entered the room. After this short period of aggressiveness, however, they slowly became more docile. The disposition shown by the newborn young is clearly an innate behavioral pattern that undoubtedly has a direct relationship to survival. The majority of cotton-

mouths that I have approached in the field have moved swiftly to seek refuge in nearby water; a few have remained motionless as I approached, and one showed the typical threat display. Upon capture and handling, they react similarly to other pit-vipers by opening and closing the mouth and erecting the fangs in an attempt to bite. They often bite through the lower jaw and eject venom at this time as well as when the mouth is open. Of more than a dozen individuals kept in captivity, four were particularly difficult to handle whereas another was extremely docile. It was almost never found in aggregations with the other snakes and did not struggle or attempt to bite when handled. The majority remained unpredictable in disposition, usually appearing docile and lazy but capable of extremely rapid movements when disturbed.

Defense and Escape

The typical threatening posture of rattlesnakes is all but lacking in the cottonmouth, which relies primarily on concealing coloration or nearness to water for escape. When approached, it usually plunges into nearby water or remains motionless with the head held up at a 45° angle and the mouth opened widely exposing the white interior. The tail is sometimes vibrated rapidly and musk is expelled. This threat display is unique to cottonmouths; although it does not attract as much attention as the display of rattlesnakes, it is probably an effective warning to most intruders at close range.

Neill (1947:205) reported one case in which a cottonmouth used the "body blow" defense, described for *Crotalus* by Cowles (1938:13), when approached by a kingsnake, *Lampropeltis getulus*. In this unusual posture the anterior and posterior portions of the body are held against the ground and the middle one-fourth to one-third of the body is lifted up and used in striking the intruder. This same defense posture also was observed in rattlesnakes when presented with the odor of the spotted skunk, *Spilogale phenax*. However, the "kingsnake defense posture" is probably not a well-established behavioral pattern in the cottonmouth, for it sometimes feeds upon kingsnakes. I observed the killing and devouring of a cottonmouth by a speckled kingsnake, *L. g. holbrooki;* the only attempts to escape were by rapid crawling and biting.

Cottonmouths often squirt musk as a defensive action. The tail is switched back and forth, and musk is emitted from glands on each side of the base of the tail. The fine jets of musk are sprayed upward at about 45° angles for a distance of nearly five feet. How often this defense mechanism is used against other animals is not known, but the musky odor can frequently be detected in areas where cottonmouths are common. The odor is repulsive and, if concentrated, can cause nausea in some individuals. To me, the scent is indistinguishable from that of the copperhead.

"Head Bobbing"

"Head bobbing" in snakes has been described frequently in the literature, and many interpretations have been advanced to explain its occurrence. One of the earlier accounts was that of Corrington (1929:72) describing behavior of the corn snake, *Elaphe guttata*. Characteristic bobbing occurred when the snake was cornered, and seemingly the purpose was to warn or frighten foes. Neill (1949:114-115) mentioned the jerking or bobbing of the head in several species of snakes including the cottonmouth, and remarked that "it is ap-

parently connected with courtship and with the recognition of individuals." According to Munro (1950:88), "head bobbing" appears to be a sign of annoyance in some instances but is usually concerned with reproduction and individual recognition. Richmond (1952:38) thought that many types of head movements among not only reptiles but also birds and some mammals are a result of poor vision and serve "to delimit and orient an object that for lack of motion is otherwise invisible." Head movements undoubtedly occur in animals to facilitate accommodation, but it is obvious from Richmond's conclusions that he has never observed "head bobbing" in snakes. The term itself is grossly misleading and should be discarded. Mansueti (1946:98) correctly described the movements as spastic contractions of the body. I have observed numerous instances of these movements in cottonmouths, copperheads, and rat snakes (*Elaphe obsoleta*); and in no case has the movement resembled a head bob as is described in lizards and other animals. The movement appears to be a result of a nervous or sexually excited state and consists of highly spastic contractions confined to the anterior part of the snake most of the time but affecting the entire body on some occasions.

I found the response to be most common among cottonmouths in confinement when food was introduced to a cage containing several individuals (increasing the tendency to strike at a moving object) and when an individual was placed back in the cage after being handled. At these times the snakes that were inactive began to jerk for a few seconds. When the snake is in this seemingly nervous state, the same response is elicited by another snake crawling over it. At other times the movement of one individual causes no such response. The jerking movements appear to be released by the recognition of a nervous state in another individual and may serve to protect the jerking individual from aggressive advances of the former.

Where courtship is involved, the jerking motions are made in conjunction with writhing of the male and do not result from the same type of releaser described above.

Combat Dance

The so-called combat dance between male snakes has long been known, but its significance is still poorly understood. It was for many years believed to be courtship behavior until the participants were examined and found to be males. Carr and Carr (1942:1-6) described one such instance in two cottonmouths as courtship. In their observations, as well as those of others, copulation was never observed following the "dance" but was assumed to be the ultimate goal. After the discovery that only males participated, it was suggested that combat involved competition for mates, but the "dance" has been observed at times other than the breeding season (Ramsey, 1948:228).

Shaw (1948:137-145) discussed the combat of crotalids in some detail but drew no conclusions as to the cause of the behavior. Lowe (1948:134) concluded with little actual evidence that combat among male snakes is solely for territorial purposes. Shaw (1951:167) stated that combat may occur as a possible defense against homosexuality. One case of homosexual mating among cottonmouths was reported (Lederer, 1931:651-653), but the incomplete description seems to be of normal courtship procedure except that the "female" tried to avoid the male. Two instances of combat observed between timber rattlesnakes (*C. h. horridus*) by Sutherland (1958:23-24) were definitely

initiated because of competition for food. More observations are needed before the significance of the combat can be fully understood.

THE VENOM

Properties of the Venom

The venom and poison apparatus have developed primarily as a means of causing rapid death in small animals that are the usual prey. As a protective device against larger enemies, including man, the venom may have some value; but this was probably unimportant in the evolution of the poison mechanism. A secondary function of the venom is to begin digestion of tissues of the prey. Since food is swallowed whole, injection of digestive enzymes into the body cavity enhances digestion of the prey.

Kellogg (1925:5) described venom as a somewhat viscid fluid of a yellowish color and composed of 50 to 70 per cent proteins, the chief remaining components being water and carbohydrates, with occasional admixtures of abraded epithelial cells or saprophytic microorganisms. Salts, such as chlorides, phosphates of calcium, magnesium, and ammonium, occur in small quantities. Each of the components of snake venom has a different effect on the body of the victim. It was at first believed that there were two types of venoms: neurotoxic, which acts upon nervous tissue; and haemotoxic, which acts on blood and other tissues. It has since been found that venoms are composed of varying mixtures of both types. Fairley (1929:301) described the constituents of venom as: (1) neurotoxic elements that act on the bulbar and spinal ganglion cells of the central nervous system; (2) hemorrhagins that destroy the lining of the walls of blood vessels; (3) thrombose, producing clots within blood vessels; (4) hemolysins, destroying red blood corpuscles; (5) cytolysins that act on leucocytes and on cells of other tissues; (6) elements that retard coagulation of the blood; (7) antibactericidal substances; and (8) ferments that prepare food for pancreatic digestion. Elapid snakes tend to have more of elements 1, 4, and 6 in their venoms, while viperids and crotalids, of which the cottonmouth is one, have higher quantities of elements 2, 3, and 5. Kellogg (*loc. cit.*) stated that venom of cottonmouths contains more neurotoxin than that of rattlesnakes and not only breaks down the nuclei of ganglion cells but also produces granular disintegration of the myelin sheath and fragmentation of the conducting portions of nerve fibers.

Thus, venoms contain both toxic elements and non-toxic substances that promote rapid spreading of the venom through the body of the victim. Jacques (1956:291) attributed this rapid spreading to the hyaluronidase content of venoms.

Venom Yield and Toxicity

One of the most important yet undeterminable factors of the gravity of snakebite is the amount of venom injected into the victim. Since this volume varies considerably in every bite, attempts have been made to determine the amount and toxicity of venom produced by each species of poisonous snake. Individual yield is so variable that a large number of snakes must be milked in order to determine the average yield. Even then there remains an uncertainty as to how this amount may compare with that injected by a biting snake.

Wolff and Githens (1939b:234) made 16 venom extractions from a group

of cottonmouths in a two-year period. The average yield per snake fluctuated between 80 and 237 milligrams (actual weight), and toxicity measured as the minimum lethal dose for pigeons varied from 0.05 to 0.16 milligrams (dry weight). No decrease in yield or toxicity was evident during this period. Another group of cottonmouths from which venom was extracted over a period of five years also showed no decrease in yield or toxicity. Of 315 individual extractions the average amount obtained from each individual was 0.55 cubic centimeters of liquid or 0.158 grams of dried venom (28.0 per cent solids). The minimum lethal dosage (M. L. D.) which was determined by injecting intravenously into 350-gram pigeons was found to be 0.09 milligrams (dry weight). Each snake carried approximately 1755 M. L. D.'s of venom.

The record venom extraction for the cottonmouth was 4.0 cubic centimeters (1.094 grams dried venom) taken from a five-foot snake which had been in captivity for 11 weeks and milked five weeks earlier (Wolff and Githens, 1939a:52). The average yield of venom of cottonmouths is about three times the average yield reported for copperheads by Fitch (1960:256), a difference correlated with the greater bulk and relatively large head of the cottonmouth.

Allen and Swindell (1948:13) stated that cottonmouth venom rates third in potency, compared drop for drop to that of *Micrurus fulvius* and *Crotalus adamanteus*. Freshly dried cottonmouth venom tested on young white rats showed the lethal dose to be from 23 to 29 milligrams per kilogram of body weight. The venom of 11 one-week-old cottonmouths was found to be more potent than that of adult males. Githens (1935:171) rated *C. adamanteus* venom as being weaker than that of the copperhead (*A. contortrix*), which he rated only slightly lower than cottonmouth venom. The crotalids which he ranked more toxic than cottonmouths are: the Pacific rattlesnake (*C. viridis oreganus*) and the massasauga (*S. catenatus*). He found *A. bilineatus*, *C. durissus*, and *C. v. lutosus* to have the same toxicity as cottonmouths. Minton (1953:214) found that the intraperitoneal "lethal dose 50" (the dose capable of killing half the experimental mice receiving injections of it) was 6.36 milligrams per kilogram for copperheads. However, in later publications Minton (1954:1079; 1956:146) reported that the "lethal dose 50" for copperheads was 25.65 milligrams. Approximately the same potency was determined for cottonmouths. Several rattlesnakes that he tested showed a higher toxicity than copperheads or cottonmouths.

Criley (1956:378) found the venom of copperheads to be 6.95, nearer Minton's earlier estimate, and rated cottonmouth venom as being twice as toxic as that of copperheads. The relative toxicities of other crotalids tested, considering the cottonmouth to be one unit, were: *C. basiliscus*, 0.3; *A. contortrix*, 0.5; *C. viridis oreganus*, 1.4; *A. bilineatus*, 2.2; *C. adamanteus*, 2.3; *C. v. viridis*, 3.2; *C. durissus terrificus*, 27.5.

It can be seen from the above examples that toxicity of venoms and the resistance of the animal receiving an injection of venom is highly variable. Possibly the venom of each species of snake has greatest effect on animals of the particular group relied on for food by the snake. If that is so, the venom of cottonmouths would be expected to be more toxic when tested on fish, reptiles, and amphibians than on birds and mammals. Likewise, the venom of most species of rattlesnakes would be expected to be more virulent when injected into mammals than when injected into lower vertebrates. But, according to Netting (1929:108), species of rattlesnakes that prey on cold-

blooded animals, which are less susceptible to venoms than warm-blooded animals, are thought to have highly toxic venoms. This explanation accounts for the powerful venom of *Sistrurus catenatus;* and, in this respect, venom of cottonmouths should be highly toxic also. However, no clear-cut trends have been shown in most cases. Allen (1937) injected 250-gram guinea pigs with 4 milligrams of venom of various poisonous snakes. Survival time was recorded in order to indicate the relative potency of the venoms. Of 16 such tests *C. adamanteus* held places 1, 2, 3, 12, and 16; *Bothrops atrox* held places 4, 9, 10, and 13; and *A. piscivorus* held places 5, 7, 8, and 15. Places 6, 11, and 14 were held by three individuals of different species. No relationship to size or sex was indicated by the results of this experiment.

Susceptibility of Snakes

Numerous experiments have been conducted to determine the susceptibility of various snakes to venom. The majority of these experiments were performed to learn whether or not venomous snakes were immune to their own poison. Conant (1934:382) reported on a 30-inch cottonmouth that killed two Pacific rattlesnakes and another cottonmouth. One rattlesnake was bitten on the tail and the other on or near the head and partially swallowed. Gloyd (1933:13-14) recorded fatal effects to a rattlesnake from the bite of a cottonmouth. He also reported on the observations of three other crotalids bitten by themselves or other snakes, from which no harmful effects were observed. Allen (1937) injected several snakes with dried cottonmouth venom which was diluted with distilled water just before each injection. Four cottonmouths receiving 9, 18, 19, and 20 milligrams of venom per ounce of body weight survived, while another receiving 18.7 milligrams per ounce died after three hours. A specimen of *S. miliarius* receiving 8.3 milligrams per ounce died in about ten hours, while a *C. durissus* receiving 12.5 milligrams per ounce succumbed in 45 minutes. An alligator receiving 6 milligrams per ounce died in 14 hours. Even the snakes that survived showed some degree of swelling.

The studies of Keegan and Andrews (1942:252) show that kingsnakes are sometimes killed by poisonous snakes. A *Lampropeltis calligaster* injected with *A. contortrix* venom (0.767 milligrams per gram) died five days following the injection. This amount was more than twice the amount of *A. piscivorus* venom injected into a *L. getulus* by Allen (1937) in which the snake showed no ill effects. Keegan and Andrews (*loc. cit.*) stated that success in overpowering and eating poisonous snakes by *Lampropeltis* and *Drymarchon* may be due to the ability to avoid bites rather than to immunity to the venom. However, Rosenfeld and Glass (1940) demonstrated that the plasma of *L. g. getulus* had an inhibiting effect on the hemorrhagic action on mice of the venoms of several vipers.

One of the more extensive studies on effects of venoms on snakes is that by Swanson (1946:242-249). In his studies freshly extracted liquid venom was used. His studies indicated that snakes are not immune to venom of their own kind or to closely related species. Copperhead venom killed copperheads faster than did other venoms but took more time to kill massasaugas, cottonmouths, and timber rattlers. However, most of the snakes were able to survive normal or average doses of venom although they are not necessarily immune to it.

One of the major problems in comparing the data on toxicity of venom in studies of this type is that no standard method of estimating toxicity has been used. Swanson's (*loc. cit.*) amount of venom equaling one minim (M. L. D.?) ranged from 0.058 to 0.065 cubic centimeters. There were no different values given for each species, but the time that elapsed from injection of the venom to death represented the toxicity. There also was no attempt in his study to convert the amount of venom used into a ratio of the volume of venom per weight of snake, making the results somewhat difficult to interpret. Additional work in this field should provide for many injections into many individuals of several size classes. The studies to date have been on far too few individuals to allow statistical analyses to be accurate.

THE BITE

Effects of the Bite

Factors determining the outcome of snakebite are: size, health, and species of snake; individual variation of venom toxicity of the species; age and size of the victim; allergic or immune responses; location of the bite; and the amount of venom injected and the depth to which it is injected. The last factor is one of the most variable, owing to (1) character and thickness of clothing between the snake and the victim's skin, (2) accuracy of the snake's strike, and (3) size of the snake, since a large snake can deliver more venom and at a greater depth than can a small snake.

Pope and Perkins (1944) demonstrated that pit-vipers of the United States bite as effectively as most innocuous snakes and that a careful study of the bite may reveal the location of the pocket of venom, size of the snake, and possibly its generic identity (see Dentition). The bite pattern of the cottonmouth as well as the other crotalids showed the typical fang punctures plus punctures of teeth on both the pterygoid and mandible. Even so, a varying picture may be presented because from one to four fang marks may be present. At times in the fang-shedding cycle three and even four fangs can be in operation simultaneously.

Various authors have attributed death of the prey to the following causes: paralysis of the central nervous system, paralysis of the respiratory center, asphyxiation from clotting of the blood, stoppage of the heart, urine suppression due to crystallized hemoglobin in the kidney tubules, dehydration of the body following edema in the area of the bite, or tissue damage. Mouths of snakes are reservoirs for infectious bacteria, which are especially prolific in damaged tissue. Bacterial growth is aided by the venom which blocks the bactericidal power of the blood.

Three grades in the severity of snakebite (I, minimal; II, moderate; and III, severe) were described by Wood, Hoback, and Green (1955). Parrish (1959:396) added a zero classification to describe the bite of a poisonous snake in which no envenomation occurred. Grade IV (very severe) was added by McCollough and Gennaro (1963:961) to account for many bites of the eastern and western diamondback rattlesnakes.

The first symptom of poisonous snakebite is an immediate burning sensation at the site of the bite. Within a few minutes the loss of blood into the tissues causes discoloration. Swelling proceeds rapidly and can become so great as to rupture the skin. Pain is soon felt in the lymph ducts and glands. Weak-

ness, nausea, and vomiting may ensue at a relatively early stage. Loss of blood into tissues may spread to the internal organs. In conjunction with a rapid pulse, the blood pressure and body temperature can drop. Some difficulty in breathing can occur, especially if large amounts of neurotoxin are present in the venom. In severe cases the tension due to edema obstructs venous and even arterial flow, in which case bacteria may multiply rapidly in the necrotic tissue and gangrene can occur. Blindness due to retinal hemorrhages may occur. Symptoms of shock may be present after any bite.

Treatment

Perhaps one of the most important factors in the outcome of snakebite is the treatment. Because of the variable reactions to snakebite, treatment should vary accordingly. Many methods have been proposed for treating snakebite, and there is disagreement as to which is the best. The list of remedies that have been used in cases of snakebite includes many that add additional injury or that possibly increase the action of the venom. The use of poultices made by splitting open living chickens and the use of alcohol, potassium permanganate, strychnine, caffeine, or injection of ammonia have no known therapeutic value, and may cause serious complications. The most important steps in the treatment of snakebite are to prevent the spread of lethal doses of venom, to remove as much venom as possible, and to neutralize the venom as quickly as possible.

It is generally agreed that the first step in snakebite treatment should be to place a ligature above the bite to restrict the flow of venom, and also to immobilize the patient as much as possible. The ligature should be loosened at least every fifteen minutes. The next steps are sterilization of the skin and the making of an incision through the fang punctures. As pointed out by Stahnke (1954:8), the incision should be made in line with the snake's body at the time of the bite, so as to account for the rearward curvature of the fangs and possibly to reach the deposition of venom. Many instruction booklets and first-aid guides have specified the length and depth of incision to be made, but the actual size and depth of the cut should depend upon the location of the bite. An "X" cut or connection of the fang punctures is likely to facilitate the spread of the venom. No cut should be made that would sever a large blood vessel or ligament.

Extensive damage is often caused by well-meaning individuals whose attempts at first aid result in brutally deep incisions and tourniquets applied too tightly and for too long a period of time; the resultant damage in many instances exceeds that of the bite itself (Stimson and Engelhardt, 1960:165). Stimson and Engelhardt also think that time should be sacrificed to surgical cleanliness, and incisions should not be made if a hospital can be reached within an hour.

The ligature-cryotherapy (L-C) method proposed by Stahnke (1953) has been severely criticized by other workers. He stated that the ligature should be tight enough to restrict completely the flow of venom until the temperature of the area can be lowered sufficiently to prevent any action of the venom. After 10 minutes the ligature may be removed and the bitten area kept immersed in a vessel of crushed ice and water. If the envenomized member is to be treated for more than four hours (which is the case with almost all

pit-viper bites), it should be protected by placing it in a plastic bag. The venom action should be tested after 12 or more hours. This consists of a brief warming period to determine whether or not the action of the venom can be felt. The patient should be kept warm at all times; and the warming at the termination of treatment should be done gradually, preferably by allowing the water to warm slowly to room temperature.

Advocates of the L-C method warn against making incisions unless they are absolutely necessary, the theory being that each cut permits additional bacterial infection and does little good in removing venom. However, McCollough and Gennaro (1963:963) demonstrated that, in bites where the fangs had only slightly penetrated the skin, more than 50 per cent of the venom was removed in some instances if suction was started within three minutes after the injection. With deeper injection the amount of venom recovered sometimes reached 20 per cent of the dose. Stahnke suggested that an incision be made at the site of the bite only after the site has been refrigerated for at least 30 minutes.

Stimson and Engelhardt (*loc. cit.*) stated that two constricting bands should be used between the bite and the body and that cracked ice in a cloth should be applied to the bite before reaching a hospital. In addition, they suggested the following procedure. Rings of incisions should follow the swelling, and suction should continue for several hours. After the edema has receded, the limb should be wrapped in a towel containing crushed ice. Antivenin should be given only in severe cases. Calcium gluconate and gas gangrene antitoxin as well as antibiotics are helpful.

The most recent and up-to-date summary of snakebite treatment is that by McCollough and Gennaro (1963). Following is a brief summary of their suggestions:

1. Immobilization—Systemic immobilization is effected by body rest and locally by splinting the bitten area.

2. Tourniquet—A lightly occlusive tourniquet during a 30- to 60-minute period of incision and suction would seem to possess some advantages. In severe cases where medical attention is hours away, a completely occlusive tourniquet may be necessary to prevent death. Sacrifice of the extremity may be necessary for the preservation of life.

3. Incision and suction—Suction should begin three to five minutes after injection of venom if symptoms of poisoning are present. Incisions one-fourth inch to an inch long across each fang mark should be made in order to open the wound for more efficient suction. Multiple incisions are not useful for the removal of venom but may be employed under hospital conditions to reduce subcutaneous tensions and ischemia.

4. Cryotherapy—An ice cap over the site of the bite for relief of pain would seem to be permissible, especially prior to the administration of antivenin. It must be remembered that cooling during the administration of the antivenin radically reduces the access of the antiserum to the bite area.

5. Antivenin—Antiserum is the keystone to the therapy of snakebite. Careful evaluation of the severity of the bite and the patient's sensitivity should be made before the use of antivenin. In Grade II (moderate) bites, the intramuscular injection on the side of the bite may suffice. In Grades III (severe) and IV (very severe), shock and systemic effects require intravenous injection. In bites producing symptoms of this severity, antivenin must be given in

amounts large enough to produce clinical improvement. Ten to 20 units may be necessary to prevent the relapse that sometimes occurs after small doses of antivenin. Permanent remission of swelling and interruption of necrosis are the therapeutic end point in the clinical use of the antiserum.

In all cases of snakebite where there is any doubt as to the snake's identity, it should be killed if possible and taken to the hospital for positive identification. In many instances of actual bites by poisonous snakes the only treatment needed was an injection of tetanus antitoxin or toxoid and sedation, because physical examination revealed no indication of poisoning (Stimson and Engelhardt, *loc. cit.*).

Case History of a Bite

On July 29, 1963, at 8:20 a.m., I was treating a nine-month-old cottonmouth for mites. As I dropped the snake into a sink, it twisted its head and bit the tip of my right middle finger with one fang. The fang entered just under the fingernail and was directed downward, the venom being injected about five millimeters below the site of fang penetration. After placing the snake back in its cage, I squeezed the finger once to promote bleeding, wrapped a string around the base of the finger, and drove to Watkins Memorial Hospital on the University of Kansas campus. I began to feel a burning sensation in the tip of the finger almost immediately. Upon my arrival at the hospital, an additional ligature was placed around my wrist. At 8:30 a.m. a small incision was made in the end of the finger, which by this time was beginning to darken at the point of venom deposition. I sucked on the finger until 8:35 a.m., when a pan of ice water that I had requested was brought to me. No pain was felt except that caused by the ice. Fresh ice was added as needed to keep the temperature low. By 9:30 a.m. the finger had swollen and stiffened. At 10:00 a.m. the swelling had progressed to the index finger and back of the hand. I experienced difficulty in opening and closing the hand. Blood oozed slowly from the incision. A dull ache persisted and about every two to four minutes a sharp throb could be felt until nearly 11:00 a.m., when the pain diminished. The rate and intensity of throbbing increased whenever the hand was removed from the ice bath for more than a few seconds. Although only the hand was immersed, the entire forearm was cold. Pain was felt along the lymphatics on top of the arm when it was touched, and by 1:00 p.m. a slight pain could be felt in the armpit. Since swelling and pain were almost nonexistent by 2:00 p.m., I was permitted to leave. After walking to a nearby building, I again felt a burning sensation as the hand warmed. I made another ice bath and again immersed the hand in it until 4:10 p.m., at which time it was removed from the water. The pain and swelling began anew, and the hand was placed back in an ice bath from 5:30 p.m. until about 7:30 p.m. At this time cryotherapy was discontinued. From 10:00 p.m. to 12:00 midnight my legs twitched periodically, and pain could be felt in both armpits. A slight difficulty in breathing also was experienced for a short time. The acute pain and burning sensation remained in the finger until the following morning, but swelling progressed only as far as the wrist. The only discomfort that day was in the finger. The tip was darkened, the entire first digit red and feverish, and the lymphatics still painful when touched. By the third day the swelling had regressed. The incision itself was the main cause of discomfort, and the soreness at the site of the bite persisted for at least four days.

Although the L-C method of snakebite treatment has been vigorously attacked by many, there is still need of much more data before it can be unequivocally condemned or praised. It was preferred in the treatment of this bite because: I knew that envenomation was minimal and that there would be no need for antivenin; only one fang of a snake less than one foot long had entered the tip of the finger; the snake had bitten three frogs in the previous

two days and had possibly used up a considerable amount of its venom; the venom was deposited at such a shallow depth that at least a portion of it could be removed by suction; and the wound bled freely even before suction was applied. The ice water was uncomfortably cold but was not cold enough to cause frostbite, a major objection to the L-C method. Ideally, fresh ice should be added little by little to replace that which is melting, and the immersed area should be protected from the water by a plastic bag. Pain and swelling can be minimized by cryotherapy, but I would recommend its use only in cases of mild poisoning such as the one described herein.

Snakebite in the United States

Many estimates have been made of the number of bites of poisonous snakes that occur annually in the United States. The occurrence of poisonous snakebite has been nearly as badly underestimated as fatal results of their envenomations have been overrated. For important data on number of persons bitten by poisonous snakes in the United States, see the following: Allen and Swindell (1948:15); Githens (1935:172); Klauber (1956:811); Parrish (1963); Sowder and Gehres (1963:973); Stimson and Engelhardt (1960:153); Swaroop and Grab (1956:441); Swartzwelder (1950:579); Willson (1908:530); and Wood (1954b:937).

Judging from estimates made in several states, the number of poisonous snakebites in the United States would be about 5000 per year. In the region where the cottonmouth occurs there are approximately 2000 persons bitten annually by poisonous snakes. Of these approximately 39 per cent are copperhead bites, 30 per cent each are cottonmouth and rattlesnake bites, and 1 per cent are coral snake bites. These percentages vary considerably from place to place, because of the distribution and abundance of the eight species of poisonous snakes whose ranges overlap that of the cottonmouth.

According to Parrish (1963), about 14 people die of snakebite each year in the United States. Of these deaths, about 6.6 per cent are attributable to cottonmouths, 77.0 per cent to rattlesnakes, and 1.6 per cent to coral snakes; 14.8 per cent are unidentified. Almost half of the fatalities are in persons less than 20 years of age, the high mortality rate being partially due to the greater ratio of venom to body weight.

SUMMARY

In my study, 306 living and preserved cottonmouths were examined. This species occurs throughout the coastal plains of the southeastern United States, usually at altitudes of less than 500 feet but occasionally up to altitudes of more than 2000 feet.

Two subspecies are recognized: the eastern cottonmouth, *A. p. piscivorus*, occurring from extreme eastern Mississippi to southeastern Virginia and Florida; and the western cottonmouth, *A. p. leucostoma*, occurring from eastern Mississippi northward to southern Illinois and Missouri and westward to central Texas. Intergradation occurs in eastern Mississippi.

The northern edge of the range is probably limited by low temperatures in winter, and the western edge by lack of available habitat resulting from insufficient precipitation. Old records of occurrence indicate that the range has decreased in the last 100 years. The species inhabits mostly areas where water is found, but at times wanders a mile or more from the nearest water.

The ground color is predominantly a brown, but varies from a brownish-green to almost black with a pattern of 10 to 17 irregular bands of a darker shade of brown. The pattern is better defined in the eastern subspecies than in the western.

The scutellation resembles that of other species of *Agkistrodon*. In the specimens examined supralabials ranged from 7 to 9, and infralabials from 8 to 12. The number of dorsal scale rows on the neck, at mid-body, and immediately anterior to the anus is relatively constant at 27-25-21, respectively. Ventral scales of 34 males averaged 134.4 (128 to 139), and those of 48 females 133.5 (128 to 137). The number of caudal scales showed some degree of sexual dimorphism; the average was 45.4 (41 to 50) in 34 males and 42.6 (39 to 49) in 44 females. In general, caudal scales on the basal half of the tail are undivided, whereas those on the distal half are divided. No marked geographical variation was found in any scale character.

The poison fangs vary in length from 1.3 per cent of snout-vent length in juveniles to 1.0 per cent in large adults. Fangs of captive cottonmouths were shed and replaced at intervals of about 21 days, but the interval was variable. Relationships in distance between the base of fangs and between fang punctures in an actual bite indicate that examination of the wound does not provide a good basis for judging accurately the size of the snake that inflicted the bite.

In general, females less than 450 millimeters in snout-vent length were juveniles; those more than 450 millimeters were classified as postpartum or reproductive on the basis of sizes of ovarian follicles. Since about half the adult females were fecund, it was concluded that a biennial reproductive cycle occurs in this species. An annual cycle may occur in areas where temperature permits year-round activity. It was estimated that females become sexually mature at an age of approximately two and one-half years. Mating is probably most concentrated in early spring at about the time when females ovulate, but copulation is not a stimulus for ovulation. Sperm retention and delayed fertilization allow young to be produced with-

out copulation occurring in each breeding season. The testes increase in size gradually rather than rapidly at maturity or in each breeding season, but seasonal cycles in sperm production occur.

The gestation period is three and one-half to four months. Determination of sex in the embryos is possible by late June, because the hemipenes of males are evaginated until the time of birth. Parturition generally occurs in August or September, but captivity may delay birth for a month or more. From one to 16 young per litter are born, depending on size of the mother and other factors; but the average is between six and seven. Mortality rate at birth is high in captive individuals but has not been determined in natural populations. The sex ratio in embryos and adults examined revealed about 53 per cent females. Because sufficient information on population composition is not available, an estimate of the percentage of adults in a natural population was based upon the number found in my study. The reproductive potential was estimated from these figures.

Normal young at birth are 230 to 240 millimeters in snout-vent length, but their size is influenced by the condition of the mother. Comparison of newborn young with those captured in spring indicates that little growth occurs during winter. Early growth is largely dependent upon feeding before winter quiescence.

The umbilical cord is broken at birth and the navel closes within a few days, but the scar remains throughout life. Sexual dimorphism in the position of the scar is characteristic of some snakes but is minimal in cottonmouths.

In those snakes more than 700 millimeters in length, males outnumber females three to one. The maximum age of cottonmouths in nature is unknown, but one has been kept in captivity for more than 18 years.

Allometric growth is striking in cottonmouths. The head and tail are proportionately longer in young individuals than in adults; and in males the tail is, on the average, slightly longer than in females of the same size.

Shedding of the skin provides for growth and wear in snakes. The young shed within a few days after birth and generally shed more frequently than adults. Frequency of shedding depends mostly on amount of food consumed, and there is some evidence that injuries on the head and neck increase the frequency of shedding. Before shedding, the eyes become cloudy for about five

and one-half days, then clear up again for about four days before the skin is shed.

The food of cottonmouths consists mainly of small vertebrates and occasionally invertebrates that are found near water. Fish, amphibians, and reptiles make up nearly 70 per cent of the diet. Carrion is also eaten and cannibalism occurs occasionally. Food is obtained by lying in ambush or by active searching. The young are known to lure their prey within striking range by waving their yellow tails in a manner suggestive of writhing grubs. The method of obtaining prey differs according to the kind of prey. Generally, cottonmouths retain their hold on fish or frogs but release mice and larger prey after delivering a bite.

The major causes of mortality of cottonmouths are obscure. Predators are known to include alligators, indigo snakes, kingsnakes, largemouth bass, and blue herons; there are probably numerous others. Heavy parasitic infestations were found among the snakes examined. Snake mites, *Ophionyssus natricus,* became increasingly abundant on almost all captive snakes in April and May of 1963. Lung flukes (*Ochetosoma* sp.) were in 16 of 20 captive snakes, and many preserved specimens contained nematodes (*Kalicephalus* sp.) in the stomach and/or tapeworms (*Ophiotaenia* sp.) in the intestine. Although parasitic infestation causes discomfort and may lower resistance to other detrimental factors, it is difficult to attribute death to the effect of any particular kind of parasite. Miscellaneous causes of death of some captive snakes also were discussed.

The maximal body temperatures tolerated by four cottonmouths were between 38° and 40° C., but a temperature of 38° was lethal to a fifth individual. Cottonmouths have been found on occasion when other snakes were inactive because of low temperatures, but minimal temperatures tolerated by this species are not known. The annual cycle of activity is dependent upon temperature and thus varies from north to south. Cottonmouths generally migrate inland in autumn, usually to dry forested hillsides, where they den along with other species of snakes. After a few warm days in spring they migrate back to the water's edge. The diel activity cycle likewise depends upon temperatures but is influenced by other factors as well. In spring and autumn, the snakes are active mostly on warm, sunny days, whereas in summer they are active mostly at night. In order to maintain adequate internal temperatures, much

time is spent basking mostly in a characteristic flat, resting coil either beside a body of water or above water on limbs of dead trees. In this position the snake is ready either for a short strike or a hasty getaway.

Juveniles appear particularly aggressive and strike repeatedly when approached, a behavioral pattern definitely favoring survival. Adults vary in disposition, usually appearing sluggish and lazy, but they are capable of striking rapidly when disturbed. The typical threat display consists of lying in a coiled position with the mouth opened widely, exposing the white interior, and with the tail vibrating rapidly. The striking posture resembles the resting coil except that the anterior part of the body is raised off the ground and the mouth is sometimes opened. Musk is often ejected in a fine spray from glands in the tail as a further defensive action.

"Head bobbing," more properly described as spastic contractions of the body, was observed in captives when food was introduced into a cage containing several individuals or when one of the snakes was returned to the cage after being handled. Reports in the literature also have connected these jerking movements with courtship. The response appears to be elicited whenever a nervous state is recognized in another individual and may serve to protect the jerking individual from aggressive advances of the former.

The relatively heavy appearance of the body, sluggish habits, and cryptic coloration are correlated with the development of venom and fangs. The poison apparatus has developed primarily as a means of causing rapid death in prey and secondarily, perhaps, to begin the digestion of small animals that are the usual prey, but it is also important as a defensive device. The venom contains at least eight constituents that aid in its action on prey. Toxicity of the venom is difficult to determine because of numerous variables, but cottonmouth venom is generally believed to be less potent than that of most rattlesnakes and more potent than that of the copperhead. Snakes in general are more resistant to snake venoms than other vertebrates of similar size, but there is no immunity even to their own venom.

About ten per cent of the approximately 5000 bites of poisonous snakes per year in the United States are attributable to cottonmouths, and about seven per cent of the approximately 14 deaths per year are caused by cottonmouths.

LITERATURE CITED

ALLEN, E. R.
1937. Florida snake venom experiments. Florida Acad. Sci., 2:7 pp.

ALLEN, E. R., and SWINDELL, D.
1948. Cottonmouth moccasin of Florida. Herpetologica, 4:1-16 (first supplement).

ALLEN, M. J.
1932. A survey of the amphibians and reptiles of Harrison County, Mississippi. Amer. Mus. Novit., 542:1-20.

ANDERSON, P.
1941. The cottonmouth in northern Missouri. Copeia, 1941(3):178.
1945. New herpetological records for Missouri. Bull. Chicago Acad. Sci., 7(5):271-275.

ANON.
1953. Snake collecting hobby of Colonial Heights lad. Virginia Wildlife, 14:24.

AUFFENBERG, W.
1963. The fossil snakes of Florida. Tulane Studies Zool., 10(3):131-216, 51 figs.

BAILEY, R. M.
1948. Winter mortality in the snake *Storeria dekayi*. Copeia, 1948(3): 215.

BARBOUR, R. W.
1956. A study of the cottonmouth, *Agkistrodon piscivorus leucostoma* Troost, in Kentucky. Trans. Kentucky Acad. Sci., 17(1):33-41, 1 fig.

BLANCHARD, F. N.
1922. The amphibians and reptiles of western Tennessee. Occ. Pap. Mus. Zool.; Univ. Michigan, 117:1-18.

BOGERT, C. M.
1943. Dentitional phenomena in cobras and other elapids with notes on adaptive modifications of fangs. Bull. Amer. Mus. Nat. Hist., 81(3):285-360.

BRATTSTROM, B. H.
1954. The fossil pitvipers (Reptilia: Crotalidae) of North America. Trans. San Diego Soc. Nat. Hist., 12(3):31-46, 2 figs.

BROWN, A. E.
1903. Texas reptiles and their faunal relations. Proc. Acad. Nat. Sci. Philadelphia, pp. 543-558.

CARPENTER, C. C.
1958. Reproduction, young, eggs, and food of Oklahoma snakes. Herpetologica, 14:113-115.

CARR, A. F., JR.
1936. The gulf-island cottonmouths. Proc. Florida Acad. Sci., 1:86-90.

CARR, A. F., JR., and CARR, M. H.
1942. Notes on the courtship of the cottonmouth moccasin. Proc. New England Zool. Club, July 18, 20:1-6.

CLARK, R. F.
1949. Snakes of the hill parishes of Louisiana. Jour. Tennessee Acad. Sci., 24(4):244-261.

Conant, R.
1933. Three generations of cottonmouths, *Agkistrodon piscivorus* (Lacépède). Copeia, 1933(1):43.
1934. Two rattlesnakes killed by a cottonmouth. Science, 80(2078):382.
1958. A field guide to reptiles and amphibians. Houghton Mifflin Co., Boston, 366 pp.

Cook, F. A.
1962. Snakes of Mississippi. Mississippi Game and Fish Comm., Surv. Bull., ii + 45 pp.

Corrington, J. D.
1929. Herpetology of the Columbia, South Carolina region. Copeia, 1929:58-83.

Cowles, R. B.
1938. Unusual defense postures assumed by rattlesnakes. Copeia, 1938(1):13.

Cowles, R. B., and Bogert, C. M.
1944. A preliminary study of the thermal requirements of desert reptiles. Bull. Amer. Mus. Nat. Hist., 83(5):263-296.

Criley, B. R.
1956. Development of a multivalent antivenin for the family Crotalidae. Pp. 373-380 *in* Venoms (ed. Buckley, E. E., and Porges, N., Amer. Assoc. Adv. Sci., Publ. No. 44).

Darlington, P. J.
1957. Zoogeography: the geographical distribution of animals. John Wiley and Sons, Inc., New York, xi + 675 pp.

Davis, D. D.
1936. Courtship and mating behavior in snakes. Zool. Series Field Mus. Nat. Hist., 20:257-290, figs. 28-34.

Didisheim, P., and Lewis, J. H.
1956. Fibrinolytic and coagulent activities of certain snake venoms and proteases. Proc. Soc. Exp. Biol. Med., 93(1):10-13.

Ditmars, R. L.
1915. The reptile book. Doubleday, Page and Co., Garden City, N. Y., xxxii + 472 pp.
1945. The reptiles of North America. Doubleday, Doran and Co., Inc., Garden City, N. Y., xvi + 476 pp., 135 pls.

Dowling, H. G.
1951a. A proposed standard system of counting ventrals in snakes. British Jour. Herp., 1(5):97-98, 1 fig.
1951b. A proposed method of expressing scale reductions in snakes. Copeia, 1951(2):131-134.

Dundee, H. A., and Burger, W. L., Jr.
1948. A denning aggregation of the western cottonmouth. Nat. Hist. Misc., Chicago Acad. Sci., 21:1-2.

Edgren, R. A.
1951. The umbilical scar, a sexually dimorphic character in *Heterodon platyrhinos*. Nat. Hist. Misc., 83:1-2.

Fairley, N. H.
1929. The present position of snake bite and the snake bitten in Australia. Med. Jour. Australia, 1(10):296-313.

FITCH, H. S.
1956. Temperature responses in free-living amphibians and reptiles in northeastern Kansas. Univ. Kansas Publ. Mus. Nat. Hist., 8(7): 417-476, 10 figs., 6 tables.
1960. Autecology of the copperhead. Univ. Kansas Publ. Mus. Nat. Hist., 13(4):85-288, pls. 13-20, 26 figs.

FORCE, E. R.
1930. The amphibians and reptiles of Tulsa County, Oklahoma, and vicinity. Copeia, 1930(2):25-39.

FOX, W.
1948. Effect of temperature on development of scutulation in the garter snake, *Thamnophis elegans atratus*. Copeia, 1948(4):252-262.

GITHENS, T. S.
1935. Studies on the venoms of North American pit vipers. Jour. Immun., 29(2):165-173.

GLISSMEYER, H. R.
1951. Symposium. A snake den in Tooele County, Utah. Egg production of the great basin rattlesnake. Herpetologica, 7(1):24-27.

GLOYD, H. K.
1933. On the effects of moccasin venom upon a rattlesnake. Science, 78(2010):13-14.
1934. Studies on the breeding habits and young of the copperhead, *Agkistrodon mokasen* Beauvois. Papers Michigan Acad. Sci., Arts and Letters, 19:587-604.

GLOYD, H. K., and CONANT, R.
1943. A synopsis of the American forms of *Agkistrodon* (copperheads and moccasins). Bull. Chicago Acad. Sci., 7(2):147-170, 16 figs.

GOODMAN, J. D.
1958. Material ingested by the cottonmouth, *Agkistrodon piscivorus*, at Reelfoot Lake, Tennessee. Copeia, 1958(2):149.

GUIDRY, E. V.
1953. Herpetological notes from southeastern Texas. Herpetologica, 9: 49-56.

HALL, H. H., and SMITH, H. M.
1947. Selected records of reptiles and amphibians from southeastern Kansas. Trans. Kansas Acad. Sci., 49(4):447-454.

HAMILTON, W. J., JR., and POLLACK, J. A.
1955. The food of some crotalid snakes from Fort Benning, Georgia. Nat. Hist. Misc., 140:1-4.

HERALD, E. S.
1949. Effects of DDT oil solution upon amphibians and reptiles. Herpetologica, 5(6):117-120.

HICKMAN, C. P.
1922. A northern record for the water moccasin. Copeia, 1922(106):39.

HURTER, J. H.
1897. A contribution to the herpetology of Missouri. Trans. Acad. Sci. St. Louis, 7:499-503.

JACQUES, R.
1956. The hyaluronidase content of animal venoms. Pp. 291-293 *in* Venoms (ed. Buckley, E. E., and Porges, N., Amer. Assoc. Adv. Sci., Publ. No. 44).

Keegan, H. L., and Andrews, T. F.
1942. Effects of crotalid venom on North American snakes. Copeia, 1942:251-254.

Kellogg, R.
1925. Poisonous snakes of the United States. U. S. D. A. Papers (371), 13 pp.

Klauber, L. M.
1941. Four papers on the application of statistical methods to herpetological problems. Bull. Zool. Soc. San Diego, 17:1-95.
1956. Rattlesnakes. Univ. California Press, 2 vols., xxix + 1476 pp.

Klimstra, W. D.
1959. Food habits of the cottonmouth in southern Illinois. Chicago Acad. Sci., Nat. Hist. Misc., 168:1-8.

Laughlin, H. E.
1959. Stomach contents of some aquatic snakes from Lake McAlester, Pittsburgh County, Oklahoma. Texas Jour. Sci., 11(1):83-85.

Lederer, G.
1931. Aus meinem Tagebuch. Wachenschrift fur Aquar. und Terr'kde., 28:651-653.

Lee, H. T.
1964. Letters to the Editor, Texas Game and Fish Mag., 22(3):32.

Lowe, C. H., Jr.
1948. Territorial behavior in snakes and the so-called courtship dance. Herpetologica, 4(4):129-145.

Mansueti, R.
1946. Mating of the pilot blacksnake. Herpetologica, 3:98-100, 1 fig.

Martin, J. R., and Wood, J. T.
1955. Notes on the poisonous snakes of the Dismal Swamp area. Herpetologica, 11(3):237-238.

McCollough, N. C., and Gennaro, J. F., Jr.
1963. Evaluation of venomous snake bite in the southern United States from parallel clinical and laboratory investigations. Jour. Florida Med. Assn., 49(12):959-967.

McIlhenny, E. A.
1935. The alligator's life history. The Christopher Publ. House, Boston, Massachusetts, 117 pp.

Minton, S. A., Jr.
1953. Variation in venom samples from copperheads (*Agkistrodon contortrix mokeson*) and timber rattlesnakes (*Crotalus horridus horridus*). Copeia, 1953:212-215.
1954. Polyvalent antivenin in the treatment of experimental snake venom poisoning. Amer. Jour. Trop. Med. and Hyg., 3:1077-1082.
1956. Some properties of North American pit viper venoms and their correlation with phylogeny. Pp. 145-151 *in* Venoms (ed. Buckley, E. E., and Porges, N., Amer. Assoc. Adv. Sci., Publ. No. 44).

Munro, D. F.
1949. Effect of DDT powder on small cottonmouths. Herpetologica, 5:71-72.
1950. Additional observations on head bobbing by snakes. Herpetologica, 6:88.

NEILL, W. T.
1947. Size and habits of the cottonmouth moccasin. Herpetologica, 3:203-205.
1949. Head bobbing, a widespread habit of snakes. Herpetologica, 5:114-115.
1960. The caudal lure of various juvenile snakes. Quart. Jour. Florida Acad. Sci., 23(3):173-200, 2 figs.

NEILL, W. T., and ALLEN, E. R.
1955. Metachrosis in snakes. Quart. Jour. Florida Acad. Sci., 18(3): 207-215.

NETTING, M. G.
1929. The venom of *Sistrurus catenatus*. Bull. Antivenin Inst. Amer., 2(4):108-109.

PARRISH, H. M.
1959. Poisonous snakebites resulting in lack of venom poisoning. Virginia Med. Month, 86:396-401.
1963. Analysis of 460 fatalities from venomous animals in the United States. Amer. Jour. Med. Sci., 245(2):35-47.

PARRISH, H. M., and POLLARD, C. B.
1959. Effects of repeated poisonous snakebite in man. Amer. Jour. Med. Sci., 237(3):277-286.

PENN, G. H.
1943. Herpetological notes from Cameron Parish, Louisiana. Copeia, 1943(1):58-59.

PERKINS, C. B.
1955. Longevity of snakes in captivity in the United States. Copeia, 1955(3):262.

POPE, C. H., and PERKINS, R. M.
1944. Differences in the patterns of bites of venomous and of harmless snakes. Archives of Surgery, 49:331-336.

RAHN, H.
1942. The reproductive cycle of the prairie rattler. Copeia, 1942(4): 233-240.

RAMSEY, L. W.
1948. Combat dance and range extension of *Agkistrodon piscivorus leucostoma*. Herpetologica, 4:228.

RICHMOND, M. D.
1952. Head bobbing in reptiles. Herpetologica, 8:38.

ROSENFELD, S., and GLASS, S.
1940. The inhibiting effect of snake bloods upon the hemorrhagic action of viper venoms on mice. Amer. Jour. Med. Sci., 199:482-486.

SCHMIDT, K. P.
1946. On the zoogeography of the Holarctic region. Copeia, 1946: 144-152.

SHAW, C. E.
1948. The male combat "dance" of some crotalid snakes. Herpetologica, 4:137-145.
1951. Male combat in American colubrid snakes with remarks on combat in other colubrid and elapid snakes. Herpetologica, 7(4):149-168.

SMITH, H. M.
1956. Handbook of amphibians and reptiles of Kansas. 2nd Edition. Univ. Kansas Mus. Nat. Hist., Misc. Publ., 9:1-356, 253 figs.

Smith, H. M., and Buechner, H. K.
1947. The influence of the Balcones Escarpment on the distribution of amphibians and reptiles in Texas. Bull. Chicago Acad. Sci., pp. 1-16.

Smith, P. W.
1961. The amphibians and reptiles of Illinois. Illinois Nat. Hist. Survey, 28(1):1-298.

Smith, P. W., and List, J. C.
1955. Notes on Mississippi amphibians and reptiles. Amer. Midl. Nat., 53(1):115-125.

Sowder, W. T., and Gehres, G. W.
1963. Snakebites in Florida. Jour. Florida Med. Assn., 49(12):973-976.

Stabler, R. M.
1951. Some observations on two cottonmouth moccasins made during 12 and 14 years of captivity. Herpetologica, 7:89-92.

Stahnke, H. M.
1953. The L-C treatment of venomous bites and stings. Amer. Jour. Trop. Med. and Hyg., 2(1):142-143.
1954. The L-C method of treating venomous bites and stings. Pois. Anim. Res. Lab., Arizona State Coll., 28 pp.

Stejneger, L.
1895. The poisonous snakes of North America. Smithsonian Inst., U. S. Nat. Mus., 1893:337-487, pls. 1-19, figs. 1-70.

Stimson, A. C., and Engelhardt, T. H.
1960. The treatment of snakebite. Jour. Occ. Med., 2(4):163-168.

Sutherland, I. D.
1958. The "combat dance" of the timber rattlesnake. Herpetologica, 14(1):23-24.

Swanson, P. L.
1946. Effects of snake venoms on snakes. Copeia, 1946(4):242-249.

Swaroop, S., and Grab, B.
1956. The snakebite mortality problem in the world. Pp. 439-466 *in* Venoms (ed. Buckley, E. E., and Porges, N., Amer. Assoc. Adv. Sci., Publ. No. 44).

Swartzwelder, J. C.
1950. Snake-bite accidents in Louisiana with data on 306 cases. Amer. Jour. Trop. Med., 30(4):575-589.

Tinkle, D. W.
1962. Reproductive potential and cycles in female *Crotalus atrox* from northwestern Texas. Copeia, 1962(2):306-313.

Trowbridge, A. H.
1937. Ecological observations on amphibians and reptiles collected in southeastern Oklahoma during the summer of 1934. Amer. Midl. Nat., 18(2):285-303.

Volsoe, H.
1944. Structure and seasonal variation of the male reproductive organs in *Vipera berus* (L.). Spolia Zool. Mus. Hauniensis V. Reprint, Copenhagen, pp. 1-172.

Wharton, C. H.
1960. Birth and behavior of a brood of cottonmouths, *Agkistrodon piscivorus piscivorus*, with notes on tail-luring. Herpetologica, 16: 125-129.

WILLSON, P.
1908. Snake poisoning in the United States: a study based on an analysis of 740 cases. Arch. Int. Med., 1(5):516-570.

WOLFF, N. O., and GITHENS, T. S.
1939a. Record venom extraction from water moccasin. Copeia, 1939(1):52.
1939b. Yield and toxicity of venom from snakes extracted over a period of two years. Copeia, 1939(4):234.

WOOD, J. T.
1954a. The distribution of poisonous snakes in Virginia. Virginia Jour. Sci., 5(3):152-167, 4 maps.
1954b. A survey of 200 cases of snake-bite in Virginia. Amer. Jour. Trop. Med. and Hyg., 3(5):936-943.

WOOD, J. T., HOBACK, W. W., and GREEN, T. W.
1955. Treatment of snake venom poisoning with ACTH and cortisone. Virginia Med. Month, 82:130-135.

WRIGHT, A. H., and WRIGHT, A. A.
1957. Handbook of snakes of the United States and Canada. Comstock Publ. Assoc., Cornell Univ. Press, 2:ix + 565-1106 pp.

YAMAGUTI, S.
1958. Systema helminthum. Interscience Publ., Inc., New York, 3 vols., 5 parts, 1:xi + 1575 pp., 2:vii + 860 pp., 3:1261 pp.

YERGER, R. W.
1953. Yellow bullhead preyed upon by cottonmouth moccasin. Copeia, 1953(2):115.

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7. Neotropical hylid frogs, genus Smilisca. By William E. Duellman and Linda Trueb. Pp. 281-375, pls. 1-12, 17 figures in text. July 14, 1966.
8. Birds from North Borneo. By Max C. Thompson. Pp. 377-433, 1 figure in text. October 27, 1966.
9. Natural history of cottonmouth moccasin, Agkistrodon piscivorus (Reptilia). By Ray D. Burkett. Pp. 435-491, 7 figures in text. October 27, 1966.

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University of Kansas
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Gaige (1926) described *Allophryne ruthveni* as a new genus and species of diminutive bufonid from British Guiana. Noble (1931) considered *A. ruthveni* to be a toothless relative of *Centrolenella* and placed the genus in the Hylidae. Gallardo (1965) suggested that *Allophryne* is a leptodactylid of uncertain affinities. Other references to the monotypic genus have consisted only of a listing of the name or of its inclusion in a key. To date the holotype and one paratype (both females) have been reported (Gaige, 1926), and the family position of the genus remains unsettled.

A male of *Allophryne ruthveni* is among the amphibians and reptiles collected in southern British Guiana by William A. Bentley in January, 1962, and deposited in the Museum of Natural History at The University of Kansas (KU). Four additional specimens (females) are in the American Museum of Natural History; only one of the latter has definite locality data.

Acknowledgments.—We are grateful to Dr. Ernest E. Williams, Museum of Comparative Zoology (MCZ) and Dr. Richard G. Zweifel, American Museum of Natural History (AMNH) for the loan of specimens. We are further indebted to Dr. Zweifel for permission to clear and stain one specimen. Dr. William E. Duellman and Linda Trueb offered many constructive criticisms. Miss Trueb executed the drawings of the skull and finger bones. Mr. Martin Wiley provided x-ray photographs of *Allophryne*.

METHODS AND MATERIALS

Six of the seven known specimens were available for study. Measurements were taken in the manner described by Duellman (1956). One specimen was cleared and stained, using the technique of Davis and Gore (1936), in order to study the skeleton. X-ray photographs were made of another specimen for comparison.

Specimens examined.—Six, as follows: BRITISH GUIANA, *Dist. Demarara:* Marudi Creek, AMNH 44749; *Dist. Equibo:* Tumatumari, MCZ 11790 (paratype); *Dist. Rupununi (Berbice):* Wai Wai Country, N of Acarahy Mountains, west of New River (2°N, 58°W), KU 69890. Also, 3 specimens from "probably British Guiana," AMNH 70108-10 (70110 cleared and stained).

SYSTEMATIC ACCOUNT

The availability of additional material and the new information pertaining to osteology permit an amplification of Gaige's (1926) description.

Genus **Allophryne** Gaige

Allophryne Gaige, Occas. Papers Mus. Zool., Univ. Michigan, 176:1, Oct. 14, 1926. Crawford, Annals Carnegie Mus., 21(1):29, 32, Nov. 14, 1931. Noble, The biology of the amphibia. McGraw-Hill, p. 510, 1931. Ruthven, Herpetologica, 1:3, July 11, 1936. Gallardo, Papéis Avulsos, 17:79, Jan. 1, 1965.

Type species.—*Allophryne ruthveni* Gaige.

Diagnosis and definition.—A genus of diminutive frogs; vomers, maxillae, and premaxillae edentate; skin of head strongly anchored to connective tissue on cranium; prepollical spine absent in males; disk of third finger larger than tympanum, smaller than eye; no humeral hook in either sex; ilia extending anteriorly beyond sacral expansions; adults attaining snout-vent length of 31 mm.; male having darkened external subgular vocal sac; skin of dorsum pustulate.

Allophryne ruthveni Gaige

Allophryne ruthveni Gaige, Occas. Papers Mus. Zool., Univ. Michigan, 176:1-3, pl. I, Oct. 14, 1926. Crawford, Annals Carnegie Mus., 21(1): 32, Nov. 14, 1931. Ruthven, Herpetologica, 1:3, July 11, 1936. Barbour and Loveridge, Bull. Mus. Comp. Zool., 96(2):64, Feb., 1946. Peters, Occas. Papers Mus. Zool., Univ. Michigan, 539:10, Sept. 19, 1952.

Holotype.—University of Michigan Museum of Zoology 63419, adult female, from Tukeit Hill, below Kaiteur Falls, Equibo District, British Guiana; obtained in May, 1924, by E. N. Clarke.

Diagnosis.—Fingers free; toes two-thirds webbed; no supernumerary tubercles on soles or palms; no tarsal fold; elongate anal sheath, anal opening on lower surface of thighs; head broad, interorbital space 2.5 times width of upper eyelid; snout subacuminate in dorsal profile, strongly sloping in lateral profile; tympanum visible in males, concealed in females; venter areolate.

External Morphology.—(Fig. 1) *Additional features not mentioned in diagnoses:* Head wider than long, about as wide as body; supratympanic fold present; canthus rostralis rounded, loreal region slightly concave, nearly vertical; nostril at tip of snout; pupil horizontal; no teeth on maxillary, premaxillary, or vomer; tongue small, round, thick, not notched behind, free posteriorly for one-sixth of length; choanae large, only partly visible from directly below; males having darkened subgular vocal sac; vocal slits present in male.

Axillary membrane lacking or but slightly developed; no tubercles or ridge under forearm; two palmar tubercles; subarticular tubercles small, simple, round, flattened; tips of fingers slightly expanded, T-shaped, with prominent transverse groove; first finger shorter than second (stated as longer than second in diagnosis by Gaige, 1926:2); folds extending laterally from anus for a short distance, then downward to venter of thighs; no appendage on heel, no inner or outer tarsal folds or tubercles; inner metatarsal tubercle oval, about twice as long as wide; outer metatarsal tubercle nearly absent; no supernumerary tubercle on sole; subarticular tubercles on foot small, round, simple, and diffuse; toes T-shaped, slightly wider than digit; toes about two-thirds webbed (Fig. 1d).

Skin of venter coarsely areolate; skin of flanks, throat, chest, undersurfaces of arms, tibia, tarsi, dorsal surfaces of thighs, tarsi, hands, and feet smooth; skin of dorsal surfaces of tibia, forearm, back, and top and sides of head having large horny pustules (sharply spinous in male).

FIG. 1. *Allophryne ruthveni,* male (KU 69890); (*a*) Dorsum. (*b*) Thenar view of right hand. (*c*) Lateral profile of head. (*d*) Plantar view of right foot. × 3.5.

Color.—Dorsum gray with irregular network of black lines and elongate blotches; flanks and labial region black with large white ocelli; dorsal surfaces of limbs gray, marked as follows: two large, elongate white spots on each thigh, concealed white spot on base of upper arm, black-edged gray transverse bars on forearms and shanks, white spot on each knee and elbow; ventral surfaces pale gray; black-edged white spot on ventral surface of thigh on each side of anal opening; chin and throat dark gray with white spots; vocal sac in male black (Fig. 1a and c).

Gaige (1926) briefly described the color, which conforms to the above in all particulars. The paratype (MCZ 11790) has lost the gray color after 40 years in preservation; now (1966) the ground-color is cream-brown, and the dorsal spotting, noted by Gaige as being black, is now brown.

The spots on the feet, tarsi, knees, thighs, flanks and upper arm are white in preservative, but in life possibly were red or yellow. These colors usually fade to white in preservative. Red or yellow spots are common aposematic colors in frogs.

Variation.—Eight measurements were taken on each specimen and four ratios were computed; these are summarized in Table 1. Gaige's illustration of the holotype shows that it has a greatly reduced pattern, whereas the paratype and three of the other five known specimens have relatively large and numerous spots. The male (KU 69890) and one female (AMNH 70108) have a reduced pattern intermediate between that of the holotype and the four other specimens.

TABLE I.—Variation in Measurements and Proportions of Allophryne ruthveni. (Ranges in parentheses below means.)

Character	Male (1)	Females (5)
Snout-vent (in mm.)	20.6	23.6 (18.4–31.0)*
Tibia/snout-vent	0.43	0.43 (0.41–0.47)
Tympanum/head width	0.12	0.15 (0.14–0.16)
Eyelid/interorbital space	0.55	0.53 (0.49–0.56)
Tympanum/eye length	0.40	0.46 (0.42–0.50)

* Holotype is reported to be 31 mm. snout-vent length (Gaige, 1926). The largest measured by us was 26.2 mm. snout-vent.

The dorsal spinules are most pronounced and extensive on the male (Fig. 1) and less so in all other specimens examined. The illustration of the holotype suggests that it has equally prominent, but fewer, spinules (Gaige, 1926).

The holotype, a gravid female, is the largest known specimen (31 mm., snout-vent length). Another gravid female (AMNH 70108) has a snout-vent length of 26.2 mm.

Distribution.—All known specimens have been found in the foothills of the northeastern face of the Guiana Massif in British Guiana.

FAMILY POSITION

The following characters of *Allophryne* are those generally held to be useful in determining family relationships:

1. Presacral vertebrae procoelus, eight in number.
2. Parahyoid absent.
3. Free ribs lacking.
4. Bidder's organ absent.
5. Intercalary cartilages present in digits; phalangeal formulae 3-3-4-4 and 3-3-4-5-4.
6. Coccyx articulating with sacrum by two condyles.
7. Tarsal bones not fused.
8. Pectoral girdle arciferal.
9. Epicoracoidal horns present, free.
10. Terminal phalanges T-shaped.
11. Sacrum procoelus and diapophyses expanded.
12. Maxillae, premaxillae, and prevomers edentate.
13. Cranial roofing bones well ossified.

Griffiths (1959) accorded considerable taxonomic weight to the presence or absence of epicoracoidal horns in showing relationships among the genera placed in the Brachycephalidae [= Atelopodidae; Dendrobatidae; and Leptodactylidae (in part)] by Noble (1931). *Allophryne* possesses well-developed, free epicoracoidal horns, such as those found in the Hylidae, Centrolenidae, Leptodactylidae and Bufonidae.

The presence of intercalary elements in the digits is characteristic of the Centrolenidae, Hylidae, Phrynomeridae, Pseudidae, and the rhacophorine ranids (including the Hyperoliidae). This element is bony in the pseudids and cartilaginous in the other families. Phrynomerids and rhacophorine ranids lack epicoracoidal horns and have firmisternal pectoral girdles. Centrolenids are small, delicate, arboreal frogs having poorly ossified skulls and fused tarsal bones, but agree with *Allophryne* in having T-shaped terminal phalanges.

Only the presence of intercalary cartilages (Fig. 2) suggests relationship of *Allophryne* to the Hylidae. The T-shaped terminal phalanges suggest affinities with centrolenids, elutherodactyline leptodactylids, or certain "brachycephalid" frogs. Griffiths (1959) clearly showed that Noble's Brachycephalidae was a polyphyletic assemblage. No hylid genus is edentate, and none has either

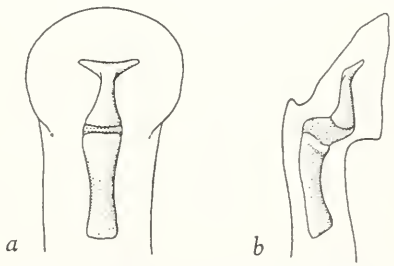

Fig. 2. Dorsal (*a*) and lateral (*b*) views of distal phalanges of third finger of *Allophryne*. × 40.

T-shaped terminal phalanges or the unusual dorsal spinules. Perhaps the presence of intercalary cartilages is not indicative of relationship but instead is a parallelism (or convergence) in *Allophryne* and genera of the Centrolenidae.

CRANIAL OSTEOLOGY

The skull of *Allophryne* (Fig. 3) is distinctive among anurans; it does not closely resemble the skulls of either hylids or centrolenids, both of which have generally more delicate (except for casque-headed hylids, such as *Corythomantis, Diaglena, Osteocephalus, Triprion*) and generalized skulls. *Allophryne* on the other hand has a strongly ossified central region (cranial roofing bones and sphenethmoid complex) and a weak peripheral zone. The peripheral elements are reduced (maxilla, pterygoid, and squamosal) or absent (quadratojugal), whereas the frontoparietals, nasals, sphenethmoid, proötics, and exoccipitals form a compact central zone. An elongate frontoparietal fontanelle is present.

Dorsally (Fig. 3), the premaxillae are not visible. The proportionally gigantic septomaxillae are visible anterior to the nasals. The moderate-sized nasals are separated medially and in broad contact with the ethmoid posteriorly. The palatine process of the nasal does not meet the frontal process of the maxilla. A large frontoparietal fontanelle is evident between the frontoparietals.

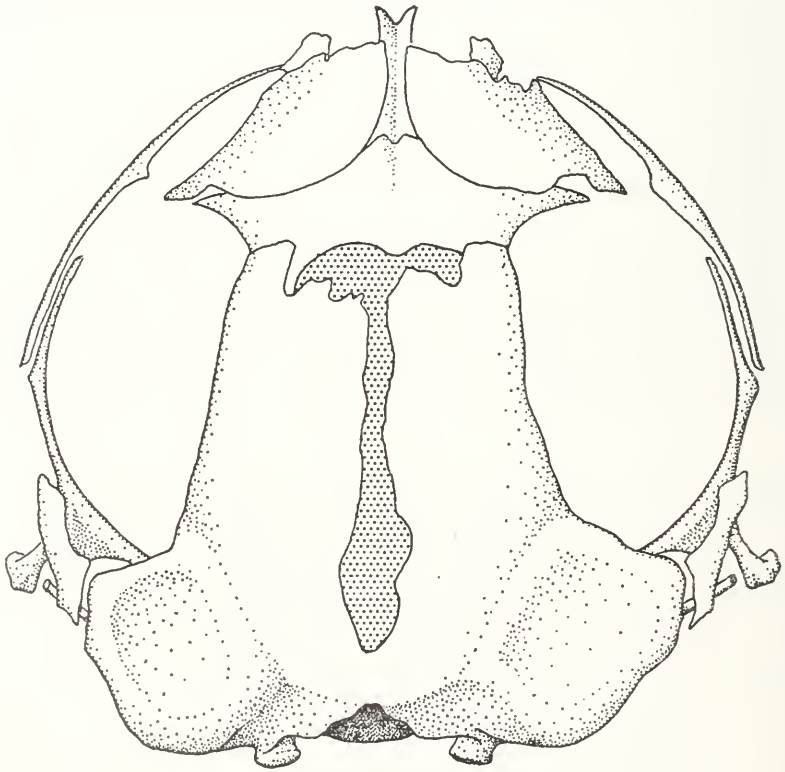

Fig. 3. Dorsal view of skull of *Allophryne* (AMNH 70110). × 12.

The tegmen tympani are much reduced and maintain only cartilaginous contact with the posterior arms of the squamosals. The foramen magnum, occipital condyles, and exoccipitals show no unusual features. The *pars facialis* and frontal process of the maxilla are greatly reduced. The maxilla and premaxilla are articulated. The high, narrow alary processes of the premaxillae extend dorsally about two-thirds of the height of the snout. A cartilaginous internasal septum is illustrated (Fig. 3), but sectioning is necessary to determine the true nature and extent of this element.

Ventrally, the skull lacks palatines. The maxillae, premaxillae, and prevomers are edentate. The parasphenoid is large with relatively short, stout alary (lateral) processes. The sphenethmoid is extensive in ventral aspect and forms the major supporting structure in the anterior part of the skull. The pterygoid has a broad articulation with the maxilla, a tenuous contact with the squamosal, but is not attached to the proötic. The anterior (zygomatic) process of the squamosal is greatly reduced (only about one-third the length of the posterior process).

DISCUSSION

The skull of *Allophryne* is definitely non-hylid. Most of the postcranial features do not help to clarify relationships. *Allophryne* shares several osteological features with the Dendrobatidae: T-shaped terminal phalanges, general cranial morphology and procoelus vertebrae. But, the dendrobatids possess firmisternal pectoral girdles and lack epicoracoidal horns. Also, no dendrobatid has intercalary elements in the digits. We are, therefore, left with a taxonomic enigma. In one or more characters generally regarded as important, *Allophryne* differs from all presently defined families of frogs. The Hylidae and Dendrobatidae are the only currently recognized families in which the genus might be placed.

The function and taxonomic importance of the large septomaxillae are unknown and are probably associated with the modification of the sphenethmoid-prevomer area. A more detailed study of the cranial osteology of *Allophryne*, especially the structural relationships of the sphenethmoid-prevomer area may elucidate the relationships of *Allophryne*.

The relationships of *Allophryne* cannot be understood without a re-analysis of some of the features used as major criteria in frog classification (the nature of an intercalated cartilage; the nature of the sternal complex; the relative value of cranial osteology; the vertebral structure; and the thigh musculature). Some of these features have been investigated by other workers, most notably Griffiths, but others have not and need re-examination. A reanalysis of some of the major criteria used in frog classification is in progress (Callison, Lynch, and Trueb) and upon completion of that study we think the relationships of *Allophryne* will become apparent.

A more comprehensive study of the cranial anatomy of certain hylids, leptodactylids, dendrobatids, and atelopodids along with that of *Allophryne* is needed to clarify the relationships of *Allophryne*, and might indicate that the recognition of a fifth family is necessary.

CONCLUSION

Among currently recognized families of frogs, *Allophryne* is least different from the Hylidae although it is our opinion that inclusion of this genus in the Hylidae probably represents an unnatural classification. However, the present evidence suggesting that *Allophryne* should be in another family is less convincing than evidence suggesting it should be in the Hylidae. We tentatively place *Allophryne* in the Hylidae.

LITERATURE CITED

Davis, D. D. and Gore, U. R.
1936. Clearing and staining skeletons of small vertebrates. Fieldiana: Technique, 4:1-16.

Duellman, W. E.
1956. The frogs of the hylid genus *Phrynohyas* Fitzinger, 1843. Misc. Publs. Mus. Zool., Univ. Michigan, 96:1-47, February 21.

Gaige, H. T.
1926. A new frog from British Guiana. Occas. Papers Mus. Zool., Univ. Michigan, 176:1-3, October 14.

Gallardo, J. M.
1965. A propósito de los Leptodactylidae (Amphibia Anura). Papéis Avulsos, 17:77-87, January 1.

Griffiths, I.
1959. The phylogeny of *Sminthillus limbatus* and the status of the Brachycephalidae (Amphibia: Salientia). Proc. Zool. Soc. London, 132: 457-87, May.

Noble, G. K.
1931. The biology of the amphibia. McGraw-Hill, New York, vii + 577 pp.

Transmitted August 2, 1966.

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Genera of Leptodactylid Frogs in México

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INTRODUCTION

According to the most recent review of the Mexican amphibian fauna (Smith and Taylor, 1948), six genera of leptodactylid frogs occur in México. One other genus, *Pleurodema,* occurs in Lower Central America. Smith and Taylor recognized one species of *Engystomops,* 28 of *Eleutherodactylus,* three of *Leptodactylus,* eight of *Microbatrachylus,* 12 of *Syrrhophus,* and five of *Tomodactylus.* Subsequent to the publication of their checklist of the Mexican amphibia (1948), numerous taxonomic changes have been proposed. Many species of *Eleutherodactylus* have been added to the fauna, either through the extension of their recorded ranges into México from Guatemala or by the recognition of species unknown in 1948, whereas some nominal species have been synonymized. *Microbatrachylus* has been regarded as synonymous with *Eleutherodactylus* (Lynch, 1965); four species of *Microbatrachylus* currently are regarded as valid (Duellman, 1961, Lynch, 1965). *Syrrhophus* was revised in part by Duellman (1958) and Firschein (1954), and a species of *Tomodactylus* transferred to *Syrrhophus* by Dixon (1957), who redefined *Tomodactylus* and added more species to the genus.

Since beginning my studies of the Mexican leptodactylids in 1962, I have become acutely aware of difficulties involved in defining the genera. A revision of *Eleutherodactylus* and a review of *Syrrhophus* are nearing completion, but prior to their publication it is desirable to redefine the genera of the Mexican leptodactylids, and in so doing recognize an heretofore unnamed genus. The definitions of *Eleutherodactylus* and *Leptodactylus* may need to be altered in the future, since both are widespread in South America and occur in the West Indies. Their definitions as given here are as precise as present knowledge permits. *Syrrhophus* and *Tomodactylus* are small assemblages that occur only in southwestern United States, México, and Guatemala.

Taylor (1952) synonymized *Engystomops* with *Eupemphix* which, although related, should be regarded as generically distinct (Gallardo, 1965). Perhaps the most conservative classification is that of Myers (1962) who, without published evidence, combined *Eleu-*

therodactylus, Syrrhophus, and the South American *Lithodytes* in a single genus.

The major problem for students working with the Mexican leptodactylids has not been the separation of *Engystomops* or *Leptodactylus* from other genera but the separation and definition of the eleutherodactyline frogs currently placed in three genera, *Eleutherodactylus, Syrrhophus,* and *Tomodactylus.* As will be shown in this paper, these are more conveniently placed in four genera. Once a fourth genus is recognized, certain phylogenetic problems disappear and a reasonable zoogeographic interpretation is possible for Middle American leptodactylid distribution.

ANALYSIS OF CHARACTERS

In México and northern Central America approximately 55 species of eleutherodactyline frogs (*Eleutherodactylus, Syrrhophus,* and *Tomodactylus*) are known. Four genera can be recognized on the basis of the nature of inguinal glands, morphology of the hands and feet, and certain osteological features.

Glands

Leptodactylids have a variety of glands that have been used as generic characters. Smith and Taylor (1948) regarded the so-called inguinal gland as a generic character in Mexican eleutherodaycty-lines. Lynch (1965) showed that *Eleutherodactylus* and *Micro-*

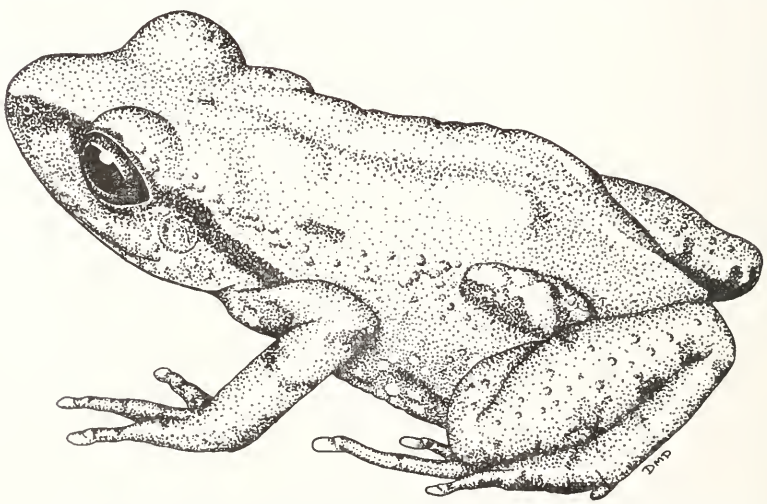

Fig. 1. *Tomodactylus angustidigitorum* (UMMZ 114305, × 4.5) illustrating the lumbo-inguinal gland typical of members of the genus. From a kodachrome by Wm. E. Duellman.

batrachylus cannot be separated by the nature of the gland or the condition of the prevomers (dentate or not). *Syrrhophus* and *Tomodactylus,* as defined by Smith and Taylor (1948), are not generically distinct because of overlap in the condition of the prevomers and in the development of the gland. Firschein (1954) stated that *Syrrhophus* differed from *Tomodactylus* by having an axillary gland, but it is now known that one species of *Syrrhophus* lacks the gland.

The inguinal glands of *Eleutherodactylus* and *Syrrhophus,* if present, are diffuse, irregular in outline, and generally not prominent; in *Tomodactylus* the gland is higher on the body (a lumbo-inguinal gland), compact, oval in outline, and prominent (Fig. 1). Axillary glands occur in most *Syrrhophus* but are not know in *Tomodactylus* or *Eleutherodactylus.*

Hands and feet

The tips of the digits are laterally expanded in most *Eleutherodactylus, Syrrhophus,* and *Tomodactylus.* Two species of *Eleutherodactylus* (*augusti* and *tarahumarensis*) and two *Tomodactylus* (*angustidigitorum* and *grandis*) lack any expansion of the digital tips. All but two of the species of eleutherodactyline frogs (*E. augusti* and *E. tarahumarensis*) have a transverse groove across the tips of the digits (Fig. 2).

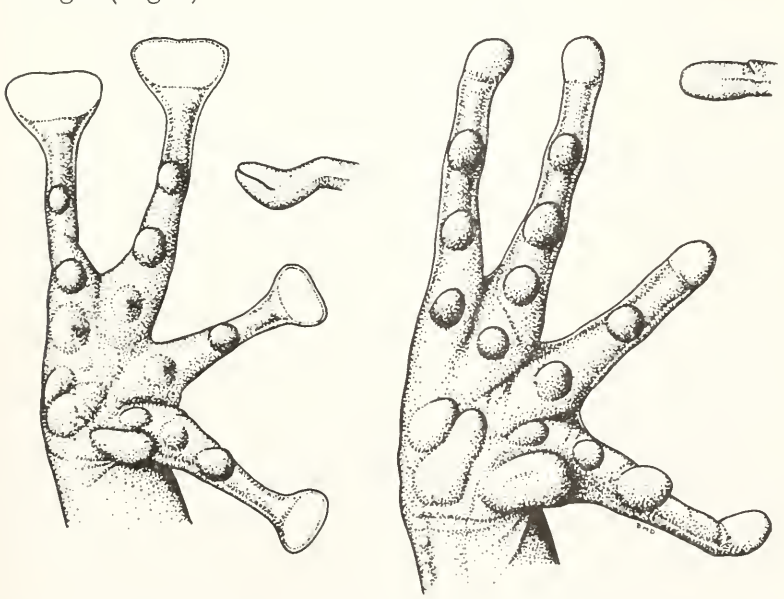

FIG. 2. Palmar views of the hands and lateral views of the tip of the third digits of *Eleutherodactylus alfredi* (left, KU 93994, × 5) and *Hylactophryne augusti* (right, KU 102594, × 3.

Supernumerary tubercles rarely are present on the feet of *Eleutherodactylus,* but are present and numerous in every species of *Syrrhophus, Tomodactylus,* and in the members of the *augusti* group of *Eleutherodactylus* (Fig. 3). The tubercles are small and numer-

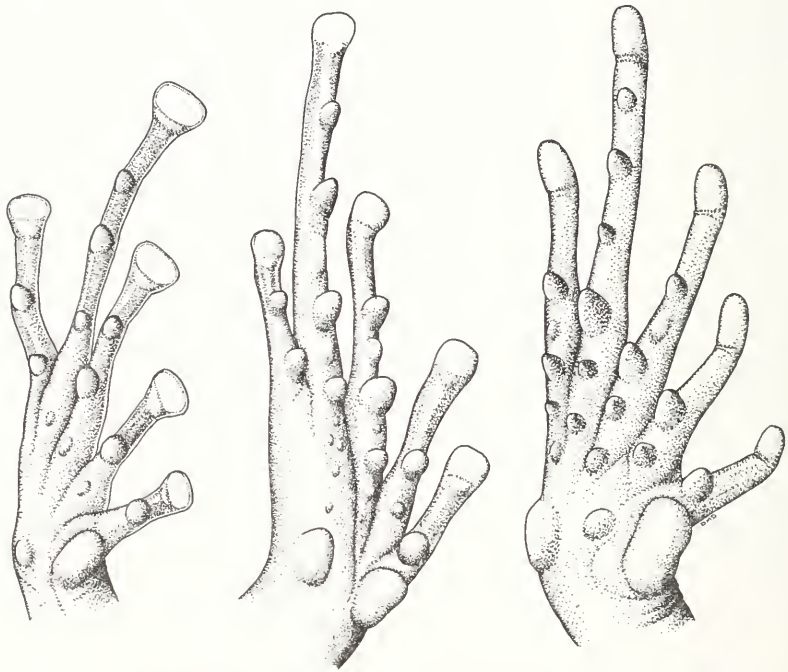

Fig. 3. Plantar views of feet of *Eleutherodactylus alfredi* (left, KU 93994, × 4.5), *Syrrhophus pipilans nebulosus* (middle, KU 58900, × 7.5), and *Hylactophryne augusti* (right, KU 102594, × 3) showing differences in size and arrangement of supernumerary tubercles.

ous in *Syrrhophus* and larger in *Tomodactylus* and the *Eleutherodactylus augusti* group. Most species of *Eleutherodactylus* have no plantar supernumerary tubercles; a few species have such tubercles, which never extend between the metatarsal tubercles as in *Syrrhophus* and *Tomodactylus.*

Tarsal folds and tubercles are lacking in *Syrrhophus, Tomodactylus,* and the *augusti* group of *Eleutherodactylus.* Several species of *Eleutherodactylus* lack tarsal folds and tubercles, but in nearly every species group, one or more species possess either an inner tarsal fold, inner tarsal tubercle(s), or outer tarsal tubercles.

The terminal phalanges of *Syrrhophus, Tomodactylus,* and all *Eleutherodactylus* (except the frogs of the *augusti* group) are dis-

tinctly T-shaped. In the latter, the bones are knob-shaped distally (Fig. 4). T-shaped terminal phalanges also are present in *Lithodytes* and *Trachyphrynus* but not in other leptodactylid genera. At least one species of *Eupsophus* (*E. quixensis*) has terminal phalanges that resemble those of the *Eleutherodactylus augusti* group.

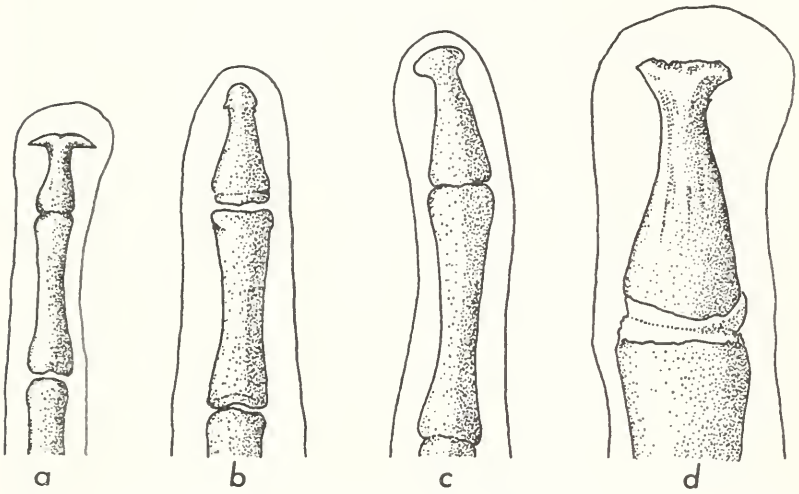

Fig. 4. Terminal phalanges of four leptodactylid frogs (all × 13.5). (a) *Eleutherodactylus mexicanus*, KU 55593; (b) *Eupsophus roseus*, KU 84731; (c) *Eupsophus quixensis*, UIMNH 59643; and (d) *Hylactophryne augusti*, KU 56192.

Several species of *Eleutherodactylus*, *Syrrhophus*, and *Tomodactylus* with slender fingers have T-shaped terminal phalanges although the terminal dilations proportionately are only scarcely wider than the finger tips in the *Eleutherodactylus augusti* group. The presence of a terminal groove at the tip of the finger is an external indicator of the T-shaped terminal phalanges.

Skull

All Mexican eleutherodactyline frogs have quadratojugal-maxillary articulations, compeltely roofed skulls in adults, median contact of the nasals, separated occipital condyles, and large prevomers. The premaxillae of all species are visible when the skulls are viewed from directly above. The pterygoid lacks a medioventral flange and does not meet the palatine. In no species is the anterior arm of the squamosal in contact with the maxillary. Of the numerous species examined (30 *Eleutherodactylus*, four *Syrrhophus*, and four *Tomodactylus*), the species in the *Eleutherodactylus augusti* group are unique in having a sphenethmoid with a blunt anterior edge.

Pectoral Girdle

All species have large cartilaginous plates in the pectoral girdles; none possesses a bony style. No divergent modifications of the clavicle and coracoid bones are known in the family.

GENERIC ACCOUNTS

Genus **Eleutherodactylus** Dumeril and Bibron, 1841

Type-species.—*Hylodes martinicensis* Tschudi, 1838

Diagnosis and definition.—Small to large frogs (12 to 110 mm. snout-vent length) having slightly to widely expanded digital pads, each pad bearing a terminal transverse groove; lumbo-inguinal, inguinal, and axillary glands absent, or if present, diffuse, irregular in outline, not compact; plantar supernumerary tubercles absent, or if present, six or fewer, restricted to distal area of plantar surface, and not extending between metatarsal tubercles; tarsus bearing inner or outer tubercles or folds or not; toes free to one-half webbed; terminal phalanges T-shaped; sternum cartilaginous, lacking bony style; sphenethmoid not truncate anteriorly; nasals in contact medially; maxillary and quadratojugal in contact; anterior arm of squamosal not in contact with maxillary; dermal cranial elements not involved in integumentary-cranial co-ossification; prevomers large, dentigerous processes present or not, dentate or not; maxillary and premaxillary bones dentate; occipital condyles separated; development direct.

Composition.—About 420 names have been applied to frogs of this genus; many of these names are synonyms, and many other species remain undescribed and unnamed. Perhaps the genus contains 350 species. Thirty-one species occur in México and northern Central America.

Distribution.—From Tamaulipas and Sinaloa, México, exclusive of the Mexican Plateau, to at least Peru and southernmost Brazil and throughout the West Indies. Introduced into Florida.

Etymology.—Greek (*eleuthero* + *dactylus*) meaning free-toed.

Genus **Engystomops** Jiménez de la Espada, 1872

Type species.—*Engystomops petersi* Jiménez de la Espada, 1872

Diagnosis and definition.—Small frogs (20 to 40 mm. snout-vent length) having undilated digital tips lacking transverse grooves; lumbo-inguinal or inguinal glands absent; plantar supernumerary tubercles present, extending between metatarsal tubercles; tarsus bearing spinelike tubercle on inner edge; toes free; terminal phalanges pointed; sternum bearing bony style; spenethmoid not truncate anteriorly; nasals in contact medially; maxillary and quadratojugal in articular contact; anterior arm of squamosal not in contact with maxillary; dermal cranial elements not involved in integumentary-cranial co-ossification; prevomers moderate in size, lacking teeth; maxillary and premaxillary bones edentate; occipital condyles separated; tadpole free living.

Composition.—Four nominal species (*E. petersi, E. pustulatus, E. pustulosus* and *E. schereri*).

Distribution.—Central Veracruz and eastern Oaxaca, México, to Trinidad, Bolivia, and Peru, east of the Andes.

Etymology.—*Greek* (*engys* + *stoma*) meaning narrow-mouthed.

Genus **Hylactophryne** new genus

Type-species.—*Hylodes augusti* Dugés, 1879

Diagnosis and definition.—Medium to large frogs (37 to 94 mm. snout-vent length) having undilated digital tips lacking terminal grooves; lumbo-inguinal or inguinal glands absent; plantar supernumerary tubercles present, prominent, extending to but not between metatarsal tubercles; tarsus lacking tubercles or folds; toes free of webbing; terminal phalanges knob-shaped, lacking elongate lateral expansions; sternum cartilaginous, lacking bony style; sphenethmoid truncate anteriorly; nasals in contact medially; maxillary and quadratojugal in articular contact; anterior arm of squamosal not in contact with maxillary; dermal cranial elements not involved in integumentary-cranial co-ossification; prevomers large, bearing dentigerous processes; maxillary and premaxillary bones dentate; occipital condyles separated; development direct.

Composition.—Two species, *H. augusti* and *H. tarahumarensis,* the former composed of four subspecies (Zweifel, 1956).

Distribution.—From Arizona, New Mexico, and Texas to Guerrero and Puebla, México, and a relict population on Cerro Quingola (just west of the Isthmus of Tehuantepec, México).

Etymology.—Greek (*hylactor* + *phryne*) meaning barking toad; in reference to the voice and common name.

Genus **Leptodactylus** Fitzinger, 1826

Type-species.—*Leptodactylus typhonia* Fitzinger, 1826

Diagnosis and definition.—Small to large frogs (30 to about 200 m.. snout-vent length) having undilated to slightly expanded digital tips bearing pads, no transverse groove at tips of digits; lumbo-inguinal, axillary, and/or ventral glands present or not, low, diffuse; plantar supernumerary tubercles generally absent, if present not extending between metatarsal tubercles; tarsus bearing tarsal folds or not; toes free of webbing, extensive lateral fringes present in some species; terminal phalanges pointed, not T-shaped; sternum bearing bony style; sphenethmoid not truncate anteriorly; nasals in contact medially; maxillary and quadratojugal in articular contact; anterior arm of squamosal not in contact with maxillary; dermal cranial elements not involved in integumentary-cranial co-ossification; prevomers large, bearing dentigerous processes; maxillary and premaxillary bones dentate; occipital condyles separated; tadpole free living.

Composition.—Sixty species according to Smith and Taylor (1948); 54 according to Gorham (1963); Argentianian authors have described several more in recent years.

Distribution.—Southern Sonora, México, and southern Texas throughout the Central and South American lowlands to Argentina. Also known from Hispaniola and Puerto Rico in the Greater Antilles and a few islands in the Lesser Antilles.

Entymology.—Greek (*leptos* + *dactylus*) meaning slender toes.

Genus Syrrhophus Cope, 1878

Type-species.—*Syrrhophus marnockii* Cope, 1878

Diagnosis and definition.—Small to medium sized frogs (18 to 40 mm. snout-vent) having slight to prominent digital expansions with transverse groove at tip of each digit; lumbo-inguinal and inguinal gland flattened, irregular in outline, not compact and oval; axillary glands present or not; plantar supernumerary tubercles numerous, more than eight, usually extending between metatarsal tubercles; tarsus lacking tubercles or folds; toes free or basally webbed; terminal phalanges T-shaped; sternum cartilaginous, lacking bony style; sphenethmoid not truncate anteriorly; nasals in contact medially; maxillary and quadratojugal in articular contact; anterior arm of squamosal not in contact with maxillary; dermal cranial elements not involved in integumentary-cranial co-ossification; prevomers large, usually lacking dentigerous processes and teeth; maxillary and premaxillary bones dentate; occipital condyles separated; development direct.

Composition.—Thirteen species; the species described as, or later referred to, *Syrrhophus* from Lower Central America and South America are *Eleutherodactylus* or *Eupsophus.*

Distribution.—Low to moderate elevations from Sinaloa, México, to Guatemala on the Pacific versant; from the Edwards and Stockton plateaus of Texas to British Honduras on the Caribbean versant.

Etymology.—Greek, emendation of *syrrhaptos,* meaning sewn together in reference to the united outer metatarsals.

Genus Tomodactylus Günther, 1900

Type-species.—*Tomodactylus amulae* Günther, 1900.

Diagnosis and definition.—Small frogs (20 to 35 mm. snout-vent length) having digital expansions or not, with transverse groove across tip of each digit; lumbo-inguinal gland prominently elevated, compact, oval, often patterned; axillary glands absent; plantar supernumerary tubercles numerous, more than eight, usually extending between metatarsal tubercles; tarsus lacking tubercles or folds; toes free; terminal phalanges T-shaped; sternum cartilaginous, lacking bony style; sphenethmoid not truncate anteriorly; nasals in contact medially; maxillary and quadratojugal in articular contact; anterior arm of squamosal not in contact with maxillary; dermal cranial elements not involved in integumentary-cranial co-ossification; prevomers large, usually bearing dentigerous processes; maxillary and premaxillary bones dentate; occipital condyles separated; development direct.

Composition.—Ten species.

Distribution.—The southern edge of the Mexican Plateau from Sinaloa to Veracruuz and onto the Oaxaca highlands and Sierra Madre del Sur.

Etymology.—Greek (*tomis* + *dactylus*) meaning knife toe; in reference to either the sharp subarticular tubercles or the unwebbed toes.

DISCUSSION

The preceding definitions only slightly alter the present generic limits of Mexican leptodactylids. Two species, previously regarded as *Eleutherodactylus,* are transferred to the new genus *Hylacto-*

phryne. The arrangement of the species of *Syrrhophus* and *Tomodactylus* remains the same as concluded by Dixon (1957), Duellman (1958), and Firschein (1954) in their reviews of the genera.

Lumbo-inguinal glands are most prominent in the genera *Pleurodema* and *Tomodactylus.* Various nondescript glands are present in many genera, but none is so well developed as those of *Pleurodema* and *Tomodactylus.*

At least nine leptodactylid genera are either known or thought to be terrestrial breeders lacking a free-living tadpole stage (*Eleutherodactylus, Euparkerella, Hylactophryne, Niceforonia, Noblella, Sminthillus, Syrrhophus, Tomodactylus* and *Trachyphrynus*). *Niceforonia* and *Trachyphrynus,* and probably *Hylactophryne,* are not closely related to the other genera. Direct development probably is an adaptation to adverse environmental conditions since many of the species occur in semi-arid or cold (Andean páramos) areas. *Eleutherodactylus* is generally thought to be the stock from which *Euparkerella, Noblella,* and *Sminthillus* evolved (Griffiths, 1959) and from which *Syrrhophus* and *Tomodactylus* are derived (Firschein, 1954).

The present distribution of *Hylactophryne* (isolated on the Mexican Plateau) and its digital form (like that of Papuan and many primitive South American leptodactylids) suggest that the genus was isolated in México throughout the Tertiary, whereas the other Central American genera are either post-Pliocene derivatives of *Eleutherodactylus* or invaders of Central America from South America since the mid-Pliocene land bridge was formed (Lloyd, 1963).

Piatt (1934) presented arguments against assigning *Eleutherodactylus latrans* to the genus *Lithodytes* and concluded that it was a "true" *Eleutherodactylus.* Contrary to his arguments, *latrans* (= *augusti* of Zweifel) and *E. tarahumarensis* Taylor differ from all other *Eleutherodactylus* (and *Syrrhophus* and *Tomodactylus*) in the nature of the tips of the digits (external and skeletal). The digits of *Hylactophryne* are like those of *Eupsophus.* My study of nearly all genera of leptodactylids indicates that Noble (1925) was correct in suggesting that *Borborocoetes* (= *Eupsophus*) is a close relative of *Eleutherodactylus latrans,* although Noble's arguments were based in part upon false evidence concerning the breeding habits of *E. latrans,* then thought to have a free-living tadpole.

Kellogg (1932) and Piatt (1934) argued that the terminal phalanges of *E. latrans* were typically eleutherodactyline. The variation of this character in *Eupsophus* (see Fig. 4) ranges from knobbed to bifurcate or Y-shaped (T-shaped in *Eleutherodactylus,*

Syrrhophus and *Tomodactylus*) and encompasses the nature of the character represented in *Hylatophryne*. *Eupsophus* differs from *Hylatophryne* in possessing a frontoparietal fontanelle, in generally having a maxillary-quadratojugal gap, and in having a free swimming tadpole stage.

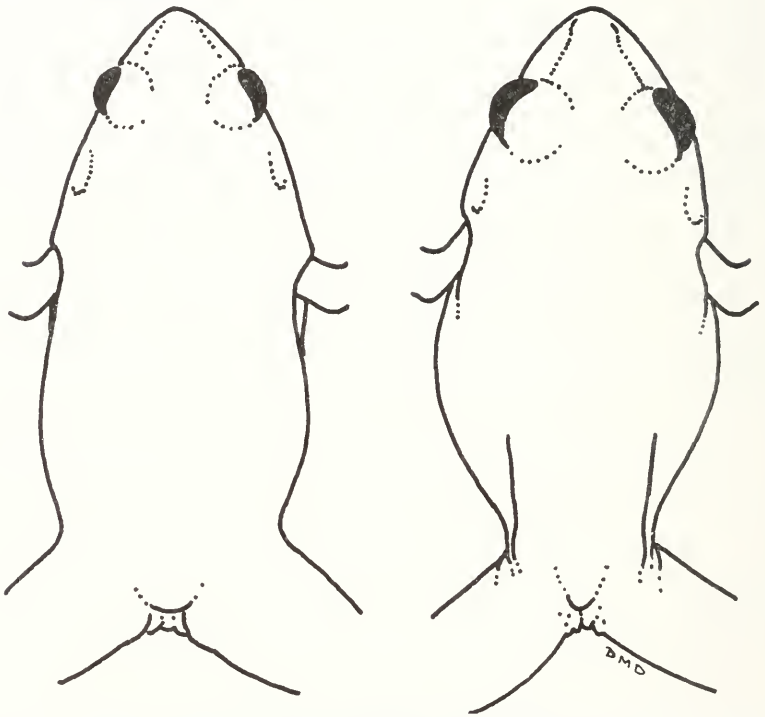

FIG. 5. Outline drawings of *Leptodactylus melanonotus* (left, KU 65704, × 2) and *Eleutherodactylus alfredi* (right, KU 93994, × 2).

KEY TO MEXICAN LEPTODACTYLID GENERA

1. Small (20-40 mm.), pustular, toadlike frogs; maxillary and premaxillary bones not bearing teeth ..... *Engystomops*
   Large (20-110 mm.), smooth skinned and non-toadlike frogs; maxillary and premaxillary bones bearing teeth 2
2. No conspicuous waist (Fig. 5); sternum bearing bony style, *Leptodactylus*
   Constrictions at waist (Fig. 5); sternum cartilaginous, no bony style .. 3
3. Few (less than six), if any, supernumerary tubercles on plantar surface ..... *Eleutherodactylus*
   Many (more than 8) supernumerary tubercles on plantar surfaces 4
4. Terminal, transverse groove across tip of digits, especially outer two fingers, digits expanded or not; small frogs (18 to 40 mm.) 5
   Tips of digits lacking transverse groove; digits unexpanded; medium-sized to large frogs (37 to 94 mm.) ..... *Hylactophryne*
5. Lumbo-inguinal gland compact, oval ..... *Tomodactylus*
   Lumbo-inguinal or inguinal gland absent or diffuse and irregular in outline ..... *Syrrhophus*

LITERATURE CITED

Dixon, J. R.
1957. Geographic variation and distribution of the genus *Tomodactylus* in Mexico. Texas Jour. Sci., 9:379-409, December.

Duellman, W. E.
1958. A review of the frogs of the genus Syrrhophus in western Mexico. Occas. Papers Mus. Zool. Univ. Michigan, 594:1-15, June 6.
1961. The amphibians and reptiles of Michoacan, Mexico. Univ. Kansas Publ. Mus. Nat. Hist., 15:1-148, December 20.

Firschein, I. L.
1954. Definition of some little understood members of the leptodactylid genus *Syrrhophus*, with a description of a new species. Copeia, 1:48-58, February 19.

Gallardo, J. M.
1965. A proposito de los Leptodactylidae (Amphibia Anura). Papeis Avulsos, 17:77-87, January 30.

Gorham, S. W.
1963. The comparative number of species of amphibians in Canada and other countries. III. Summary of species of anurans. Canadian Field-Nat., 77:13-48, March.

Griffiths, I.
1959. The phylogeny of Sminthillus limbatus and the status of the Brachycephalidae (Amphibia Salientia). Proc. Zool. Soc. London, 132:457-87, May.

Kellogg, R.
1932. Mexican tailless amphibians in the United States National Museum. Bull. U. S. Natl. Mus., 160:224 pp., March 31.

Lloyd, J. J.
1963. Tectonic history of the south Central-American orogen, *in* Childs and Beebe eds., Backbone of the Americas. Amer. Assoc. Petroleum Geol., pp. 88-100.

Lynch, J. D.
1965. A review of the eleutherodactylid frog genus *Microbatrachylus* (Leptodactylidae). Nat. Hist. Misc., 182:1-12, December 15.

Myers, G. S.
1962. The American leptodactylid frog genus *Eleutherodactylus, Hylodes* (= *Elosia*), and *Caudiverbera* (= *Calytocephalus*). Copeia, 1:195-202, April 11.

Noble, G. K.
1925. An outline of the relation of the ontogeny to phylogeny within the Amphibia. I. Amer. Mus. Nov., 165:1-17, April 16.

Piatt, J.
1934. The systematic status of Eleutherodactylus latrans (Cope). Amer. Midl. Nat., 15:89-91, February 15.

Smith, H. M. and Taylor, E. H.
1948. An annotated checklist and key to the Amphibia of Mexico. Bull. U. S. Natl. Mus., 194:1-118. June 7.

Taylor, E. H.
1952. A review of the frogs and toads of Costa Rica. Univ. Kansas Sci. Bull., 35:577-942, July 1.

Zweifel, R. G.
1956. A survey of the frogs of the *augusti* group, genus *Eleutherodactylus*. Amer. Mus. Novitates, 1813:1-35, December 23.

Transmitted July 11, 1967.

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INTRODUCTION

The small yellow tree frogs, *Hyla microcephala* and its relatives, are among the most frequently heard and commonly collected frogs in the lowlands of southern México and Central America. The similarities in size, proportions, and coloration of the different species have resulted not so much in a multiplicity of specific names, but in differences of opinion on the application of existing names to the various taxa. For example, the populations on the Atlantic lowlands have been known by three names, two of which have been applied to other taxa. Much of the confusion has been the result of previous workers' unfamiliarity with the animals in life and unawareness of the intraspecific geographic variation in the most widespread species.

Independently we undertook studies of these frogs in the field. The second author worked on the interspecific relationships and isolating mechanisms in Panamá (Fouquette, 1960b) and later studied the species in southern México. As part of his survey of the hylids of Middle America, the first author accumulated field and laboratory data on the frogs throughout their ranges in México and Central America. The purpose of this report is to present our findings on the four species of Middle American frogs that we place in the *Hyla microcephala* group. In addition to conventional taxonomic characters, we have utilized the features of the cranial osteology and have relied heavily on the data obtained from an analysis of the mating calls. Furthermore, we have included ecological and distributional data in our synthesis of interspecific relationships.

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We are grateful to many persons, too numerous to mention, who in various ways aided our field work in Middle America. We are especially indebted to Dr. Rodolfo Hernandez Corzo and the late Ing. Luis Macías Arellano of the Dirección General de la Fauna Silvestre of the Mexican government for providing permits to collect in México.

Materials and Methods

For this report, data has been obtained from 2829 preserved frogs, 42 skeletal preparations, 8 lots of tadpoles and young, and 4 lots of eggs. Much of the material was collected in our independent field work, which has extended over a period of 11 years.

Measurements were taken in the manner described by Duellman (1956). Osteological data were obtained from specimens that were cleared in potassium hydroxide, stained with alizarin red, and stored in glycerine. Recordings were made by means of Magnemite portable tape recorders (Amplifier Corp. America). The calls recorded by Fouquette were analyzed on a Sonagraph (Kay Electric Co.) at the University of Texas; those recorded by Duellman were analyzed mainly on a Vibralyzer (Kay Electric Co.) at the University of Kansas and in part on a Sonagraph at the University of Southwestern Louisiana. Sample calls were analyzed on all three instruments; the slight differences in results were found to be less than the error in measurement, so the data from all sources were combined without correction. The techniques and terminology of the calls are those defined by Fouquette (1960a, 1960b).

In the accounts of the species we have attempted to give a complete synonymy. At the end of each species account the localities from which specimens were examined are listed alphabetically within each state, province, or department, which in turn are listed alphabetically within each country. The countries are arranged from north to south. Localities preceded by an

asterisk (*) are not plotted on the accompanying maps due to the crowding of symbols that would have resulted. Abbreviations for museum specimens are listed below:

AMNH—American Museum of Natural History
ANSP—Academy of Natural Sciences of Philadelphia
BMNH—British Museum (Natural History)
BYU—Brigham Young University
CAS—California Academy of Sciences
FMNH—Field Museum of Natural History
KU—University of Kansas Museum of Natural History
MCZ—Museum of Comparative Zoology
MVZ—Museum of Vertebrate Zoology
SU—Stanford University
UIMNH—University of Illinois Museum of Natural History
UMMZ—University of Michigan Museum of Zoology
USC—University of Southern California
USNM—United States National Museum
UU—University of Utah
TCWC—Texas Cooperative Wildlife Collection
TNHM—Texas Natural History Museum

HYLA MICROCEPHALA GROUP

Definition.—Small hylids attaining a maximum snout-vent length of 27 mm. in males and 32 mm. in females; dorsum yellowish tan with brown markings; thighs uniformly yellow, vocal sac in breeding males yellow; snout truncate in lateral profile; tympanum distinct, usually slightly smaller than one-half diameter of eye; vocal sac single, median, subgular; fingers about one-third webbed; toes webbed nearly to bases of discs, except only to middle of antepenultimate or base of penultimate phalanx of fourth toe; tarsal fold weak; inner metatarsal tubercle low, flat, elliptical; axillary membrane present; pupil horizontally elliptical; palpebral membrane unmarked; cranial elements reduced in ossification; sphenethmoid small, short; frontoparietal fontanelle large; tegmen tympani not extensive; quadratojugal greatly reduced; anterior arm of squamosal extending only about one-fourth distance to maxillary; posterior arm of squamosal not having bony connection with proötic; nasals lacking maxillary processes; medial ramus of pterygoid not having bony attachment to proötic; maxillary, premaxilary, and prevomerine teeth present; palatine and parasphenoid teeth absent; Mentomeckelians ossified; tadpoles having xiphicercal tails with deep caudal fins and terminal mouth lacking teeth; mating call consisting of one primary note followed by a series of shorter secondary notes; haploid number of chromosomes, 15 (known only in *H. microcephala* and *H. phlebodes*.)

Content.—As recognized here the *Hyla microcephala* group contains four species, one having two subspecies. An alphabetical list of the specific and subspecific names that we consider to be applicable to the *Hyla microcephala* group are listed below.

Names Proposed	Valid Names
Hyla cherrei Cope, 1894	? = *H. m. microcephala*
Hyla microcephala Cope, 1886	= *H. m. microcephala*
Hyla microcephala Boulenger, 1898 (*nec* Cope, 1886)	= *H. microcephala underwoodi*
Hyla microcephala martini Smith, 1951	= *H. microcephala underwoodi*
Hyla microcephala sartori Smith, 1951	= *H. sartori*
Hyla phlebodes Stejneger, 1906	= *H. phlebodes*
Hyla robertmertensi Taylor, 1937	= *H. robertmertensi*
Hyla underwoodi Boulenger, 1899	= *H. microcephala underwoodi*

Discussion.—The color pattern is the most useful character in distinguishing the species of the *Hyla microcephala* group from one another. Except in *Hyla microcephala,* little geographic variation in color pattern is noticeable. The features of color pattern that are helpful in identifying the species are: 1) presence or absence of lateral dark brown stripe; 2) longitudinal extent and width of lateral stripe, if present; 3) presence or absence of a narrow white line just dorsal to the lateral dark stripe; 4) presence or absence of an interorbital dark mark; 5) the arrangement of dark markings on the back, either as longitudinal lines or series of dashes, or in the form of various kinds of transverse markings; 6) presence of dark flecks, longitudinal line, or transverse marks on shanks.

Few consistent differences in measurements and proportions exist among the species (Table 1). The most obvious morphological difference is that the head is noticeably narrower in *H. robertmertensi* than in the other species. *Hyla phlebodes* is the smallest species; adult males attain snout-vent lengths of only 23.6 mm. The body is slender in *H. microcephala* and *robertmertensi,* slightly wider in *phlebodes,* and noticeably broader in *sartori.*

Distribution.—The composite range of the Middle American frogs of the *Hyla microcephala* group includes the lowlands of southern México and Central America, in some places to elevations of 1200 meters, southeastward from southern Jalisco and southern Veracruz, excluding arid regions (northern Yucatán Peninsula, Balsas-Tepalcatepec Basin, Plains of Tehuantepec, Grijalva Valley, Salamá Basin, and upper Motagua Valley) to the Pacific lowlands and the Cauca and Magdalena valleys in Colombia.

Key to Species and Subspecies

1. Lateral dark stripe, bordered above by narrow white line, extending from snout at least to sacral region 2
   Lateral dark stripe, if present, not extending posteriorly to sacral region and not bordered above by narrow white line 4
2. Lateral dark stripe continuous to groin; dark flecks or longitudinal line on shanks; interorbital dark bar absent; dorsal pattern usually consisting of pair of longitudinal dark lines or series of dashes 3
   Lateral dark stripe usually extending only to sacral region; dark transverse bars on shanks; interorbital bar usually present; dorsal pattern usually consisting of interconnecting dark lines, sometimes forming transverse marks ..... *H. microcephala underwoodi*
3. Lateral dark stripe narrow, covering only upper edge of tympanum; dorsal longitudinal stripes continuous, extending to vent *H. microcephala microcephala*
   Lateral dark stripe wide, encompassing entire tympanum; dorsal markings consisting of longitudinal series of flecks or dashes, or of two lines, usually not extending to vent ..... *H. robertmertensi*

4. Lateral dark stripe indistinct, present only above tympanum and insertion of arm; dorsal markings consisting of narrow lines and dashes, sometimes interconnected; transverse bars on shanks narrow relative to interspaces ..... *H. phlebodes*

   Lateral dark stripe absent; dorsal markings consisting of two broad chevron-shaped marks; transverse bars on shanks wide relative to interspaces ..... *H. sartori*

ACCOUNTS OF SPECIES AND SUBSPECIES

Hyla microcephala Cope

Diagnosis.—Lateral dark stripe narrow, covering only upper edge of tympanum, bordered above by narrow white stripe; dorsal pattern consisting of pair of longitudinal brown lines and no interorbital bar (eastern populations), or of irregular dark markings forming an X- or) (-shaped mark in scapular region and an interorbital bar (western populations).

Content.—The populations inhabiting the Pacific lowlands of southeastern Costa Rica eastward to Colombia are recognized herein as *Hyla microcephala microcephala* Cope; the populations in western Costa Rica northward to México are assigned to *Hyla microcephala underwoodi* Boulenger.

Distribution.—Southern Veracruz and northern Oaxaca southeastward through the Atlantic lowlands of Central America to north-central Nicaragua, thence southeastward on the Pacific lowlands to eastern Panamá, and thence into the Cauca and Magdalena valleys (Caribbean drainage) of Colombia (Fig. 1).

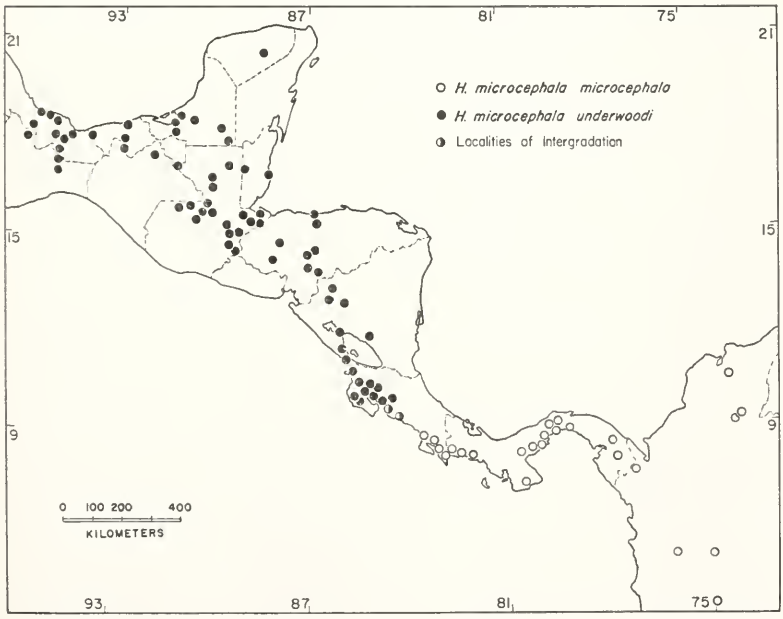


FIG. 1. Map showing locality records for *Hyla microcephala.*

TABLE 1.—Variation in Certain Measurements and Properties in the Hyla microcephala Group. (All Data Based on Adult Males; Mean and Standard Error of Mean Below Observed Range.)

LOCALITY	N	Snout-vent length (S-V L)	Tibia length / S-V L	Foot length / S-V L	Head length / S-V L	Head width / S-V L	Tympanum / Eye
				H. m. microcephala			
Panamá: Canal Zone.....	25	21.5–24.1 22.8±0.20	50.2–56.0 52.9±0.37	40.9–46.6 43.5±0.28	28.5–32.8 31.0±0.22	28.1–30.9 29.4±0.11	44.0–54.1 49.0±0.55
Costa Rica: Golfito.....	25	18.5–24.5 22.4±0.27	49.1–54.4 51.6±0.26	41.8–48.0 45.1±0.32	30.2–35.5 33.1±0.25	29.0–32.7 30.8±0.16	40.0–57.8 48.4±1.10
				H. m. underwoodi			
Nicaragua: La Cumplida...	25	23.0–25.6 21.1±0.19	51.0–55.7 52.9±0.25	41.3–46.5 43.7±0.25	29.7–33.5 31.6±0.19	28.9–31.8 30.4±0.17	42.3–60.0 49.3±0.97
Guatemala: Finca Chamá..	25	21.8–25.0 23.5±0.16	51.0–57.2 54.3±0.39	41.2–47.8 44.4±0.30	30.8–35.3 33.0±0.16	29.6–33.6 31.3±0.36	37.5–56.4 45.2±0.89
Tabasco: Teapa.....	25	22.7–25.8 24.3±0.14	48.0–54.5 51.5±0.29	40.7–46.8 43.3±0.25	29.5–33.0 31.7±0.17	28.7–31.8 30.3±0.16	40.7–53.8 45.5±0.38
Oaxaca: Donají-Sarabia....	25	22.1–25.9 23.8±0.19	49.8–55.6 52.8±0.33	40.5–46.6 43.4±0.27	30.4–34.8 32.8±0.19	28.9–32.6 30.8±0.17	37.0–54.1 45.1±0.76
Veracruz: Alvarado.....	25	21.9–25.4 21.1±0.17	49.6–54.4 51.1±0.28	40.7–47.5 42.6±0.34	29.9–33.8 31.4±0.18	29.1–32.9 30.5±0.17	40.7–53.8 46.6±0.65

LOCALITY	N	Snout-vent length (S-V L)	Tibia length / S-V L	Foot length / S-V L	Head length / S-V L	Head width / S-V L	Tympanum / Eye
				H. robertmertensi			
Guatemala: La Trinidad...	21	21.8–24.6 23.4±0.15	47.1–52.8 49.9±0.34	40.9–51.3 43.5±0.17	30.0–33.3 31.3±0.20	27.3–29.8 28.5±0.23	44.4–50.0 47.4±0.46
Chiapas: Acacoyagua.....	25	21.4–25.7 24.1±0.20	47.8–52.4 50.4±0.45	41.7–46.3 43.9±0.23	29.1–32.7 31.2±0.29	26.0–30.3 28.1±0.20	42.8–53.8 46.5±0.50
Oaxaca: Tapanatepec.....	25	22.4–26.4 24.7±0.18	44.1–48.3 46.4±0.23	39.1–44.5 41.7±0.23	26.1–30.4 28.4±0.16	25.4–28.1 26.8±0.14	45.8–58.3 52.9±0.77
				H. phlebodes			
Panamá: Canal Zone.....	25	19.6–23.2 22.2±0.16	49.1–56.9 52.8±0.35	41.9–47.1 45.4±0.26	33.6–37.4 34.8±0.18	32.3–36.0 33.8±0.18	37.9–46.4 41.6±0.49
Costa Rica: Turrialba.....	25	19.7–23.6 22.0±0.18	47.4–55.7 51.1±0.35	38.1–46.4 42.8±0.38	32.6–35.9 34.1±0.16	30.5–35.0 32.9±0.17	35.7–48.2 40.1±0.53
				H. sartori			
Guerrero: Tierra Colorada..	25	23.7–26.0 24.8±0.13	47.2–51.4 49.6±0.23	42.4–47.8 45.2±0.27	29.4–31.8 30.6±0.13	28.9–31.0 30.0±0.12	42.3–52.0 47.4±0.59

Hyla microcephala microcephala Cope

Hyla microcephala Cope, Proc. Amer. Philos. Soc., 23:281, February 11, 1886 [Syntypes.—USNM 13473 (2 specimens, now lost) from Chiriquí, Panamá; Mr. MacNeil collector]; Bull. U. S. Natl. Mus., 32:14, 1887. Günther, Biologia-Centrali Americana, Reptilia and Batrachia, p. 265, June, 1901. Dunn, Occas. Papers Boston Soc. Nat. Hist., 5:413, October 10, 1931; Occas. Papers Boston Soc. Nat. Hist., 8:72, June 7, 1933. Stebbins and Hendrickson, Univ. California Publ. Zool., 56:524, February 17, 1959. Fouquette, Evolution, 14:484, December 16, 1960. Busack, Copeia, 2:371, June 21, 1966.

? *Hyla cherrei* Cope, Proc. Acad. Nat. Sci. Philadelphia, 1894, p. 195, 1894 [Holotype.—location unknown, apparently lost; type-locality: "Alajuela, Costa Rica;" R. Alfaro collector]. Günther, Biologia Centrali-Americana: Reptilia and Batrachia, p. 264, June, 1901. Taylor, Univ. Kansas Sci. Bull., 35:846, July 1, 1952.

Hyla underwoodi, Ruthven, Misc. Publ. Mus. Zool., Univ. Michigan, 8:55, September 15, 1922. Barbour, Proc. New England Zool. Club, 10:31, March 2, 1928.

Hyla microcephala microcephala, Smith, Herpetologica, 7:185, December 31, 1951. Taylor, Univ. Kansas Sci. Bull., 39:23, November 18, 1958.

Diagnosis.—Brown lateral stripe narrow, extending from nostril along canthus, along upper edge of tympanum to groin, bordered above by narrow white line; pair of dark brown longitudinal lines on dorsum extending to vent; shanks having dark longitudinal line or flecks, no transverse bars; interorbital dark mark lacking.

Description and Variation.—The color pattern is nearly constant. Of 103 males from the Canal Zone, all lack an interorbital dark bar, and all have a dark longitudinal line on the dorsal surface of the shank and a narrow lateral dark stripe, bordered above by a narrow white line, extending to the groin. The longitudinal dark lines on the dorsum are continuous to the groin in 95 specimens and fragmented in two specimens. In two others the lines converge and fuse in the scapular region, and in four specimens auxiliary, fragmented lines are present dorsolaterally.

In all specimens from southeastern Costa Rica (Golfito, Palmar Sur, and Villa Neilly) the pattern is constant, except that in about 10 per cent of the specimens the longitudinal line on the dorsal surface of the shank is replaced by a row of brown flecks.

Of the limited number of Colombian specimens examined, all are patterned normally, except three from Sautata, Chocó, three from Curumani, and three from Arcataca, Magdalena, which have flecks on the dorsal surfaces of the shanks, and one from Espinal, Tolima, which has no markings on the shanks.

When active at night most individuals are pale yellowish tan dorsally; the white dorsolateral line is noticeable, but the brown lateral stripe, dorsal brown lines, and lines on shanks are so pale that often they are barely discernible. By day the dorsum changes to tan or pale reddish brown; the stripes are dark brown, and the dorsolateral stripe that is white at night becomes creamy yellow (Pl. 13). Small brown flecks are present on the dorsum of most individuals. The venter always is white, and the iris is pale bronze with a brown tint immediately anterior and posterior to the pupil. In breeding males the vocal sac is pale yellow.

Tadpoles.—Tadpoles of this species have been found in weed-choked ponds in eastern Panamá Province. The following description is based on KU 104097, a specimen in developmental stage 34 (Gosner, 1960).

Total length, 20.5 mm.; body length, 8.2 mm.; body slightly wider than deep; snout pointed; nostrils large, situated dorsally, much closer to snout than eyes, directed anteriorly; eyes moderately small, situated dorsolaterally and directed laterally; spiracle sinistral, located just posteroventral to eye; anal tube dextral. Tail xiphicercal; caudal musculature moderately deep, becoming slender posteriorly, extending beyond caudal fin; fins deepest at about one-third distance from body to tip of tail; dorsal fin extending onto body, deeper than deepest part of caudal musculature; ventral fin slightly shallower than musculature. Mouth small, terminal, lacking teeth and fringing papillae, but having finely serrate beaks. In preservative, top of head pale brown; dark stripe from tip of snout through eye to posterior edge of body, narrowing to thin line on proximal one-fourth of tail; venter white; tail creamy tan with fine black flecks most numerous posteriorly; posterior two-thirds of fins edged with black. In life, top of head yellowish tan; lateral stripe brown; belly white; anterior half of tail lacking pigment; posterior half deep orange; iris pale bronze (Pl. 15).

Remarks.—Evidence for intergradation of *Hyla microcephala* with *H. underwoodi* is provided by four specimens [USC 818 (2), 6081-2] from 6.1 kilometers northeast of the mouth of the Río Tarcoles, and nine specimens [USC 8254 (2), 8255, 8256 (4), 8258 (2)] from Parrita, both in Puntarenas Province, Costa Rica. These localities lie about two-thirds the distance from the northwesternmost locality for *H. m. microcephala* (Palmar Sur) to the southeasternmost locality for *H. m. underwoodi* (Barranca). Although in most aspects of coloration the frogs are more nearly like *H. m. underwoodi* than *H. m. microcephala,* some specimens have longitudinal lines on their shanks, such as are characteristic of *H. m. microcephala.* The dorsal pattern varies from nearly complete longitudinal lines to broken lines, fused into an X-shaped scapular mark or not.

As noted by Rivero (1961:135), *Hyla microcephala* seems to be closely related to *Hyla misera* Werner, a species having a wide distribution east of the Andes in South America. Despite the similarity in color pattern, size, and structure, we are reluctant to place the two taxa in the same species until data on coloration in life, mating calls, and life history are available for *Hyla misera* and compared with those of *Hyla microcephala.*

The status of Cope's *Hyla cherrei* is questionable. Since the type, the only specimen ever referred to the species, apparently is lost, the only extant information regarding the taxon is contained in the original description (Cope, 1894). There the species was characterized as having a narrow dorsolateral white stripe and lacking pigment on the upper arms and thighs. These characteristics of the color pattern combined with the statements "vomerine teeth few, opposite the middle of the very large choanae" and

"tympanic drum distinct, one half the area of eye" serve to distinguish *H. cherrei* from all other Costa Rican hylids, except *H. m. microcephala* and *H. m. underwoodi*. No statements in the type description will definitely associate *cherrei* with one or the other of these subspecies. Since it seems obvious that *H. cherrei* can be associated with *H. microcephala*, we prefer to place the name in the synonymy of the nominate subspecies, thereby preserving the commonly used name *H. underwoodi* (Boulenger, 1899) as a subspecies of *H. microcephala*.

Distribution.—*Hyla microcephala microcephala* inhabits coastal lowlands from the area of Golfo Dulce (apparently absent from the Osa Peninsula) in southeastern Costa Rica eastward in Panamá, including the Azuero Peninsula to northern Colombia and thence southward in the valleys of the Río Cauca and Río Magdalena in Colombia (Fig. 1). Except for the central area of the Canal Zone the subspecies is unknown from the Caribbean drainage in Central America, but in Colombia the subspecies occurs only in the Caribbean drainage. In Central America this frog occurs mostly on the coastal lowlands; the highest recorded elevation is 560 meters at El Valle, Coclé, Panamá. Throughout most of its range *Hyla microcephala microcephala* occurs in disturbed habitats —cut-over forests, secondary growth, and pastureland. It does not seem to be an inhabitant of either primary forest or of *Curatella*-savanna.

Specimens examined.—522, as follows: **Costa Rica:** Puntarenas: Golfito, KU 32172-207; 3 km. E Golfito, KU 86399, USC 2757-8; Palmar Sur, KU 64591-608, USC 2650 (14), UU 3907-32; °1.5-2.5 km. ESE Palmar Sur, KU 68293-7 (skeletons), 93957-62; Parrita, USC 8254 (2), 8255, 8256 (4), 8258 (2) [intergrades with *H. m. underwoodi*]; 3 km. NW Piedras Blancas, KU 103689; 6.1 km. NE mouth of Río Tárcoles, USC 818 (2), 6081-2 [intergrades with *H. m. underwoodi*]; Villa Neilly, USC 2651; °1-5 km. WNW Villa Neilly, USC 6182-4, 8003 (4), 8031 (3), 8032; °10.5 km. WNW Villa Neilly, KU 64609-27, 68398 (eggs).

Panama: Canal Zone: Albrook Air Base, TNHC 23389, 23497; Balboa, ANSP 19555-6; °Fort Clayton, UIMNH 42008-12; °2.8 km. SW Fort Kobbe, KU 96015-25; °Frijoles, MCZ 19208; °Bamboa, MCZ 21507; °8.3 km. N Gatún Locks, TNHC 23441; °Juan Diaz, MCZ 13747; °Juan Mina, AMNH 55436-7, ANSP 21811-2, UMMZ 126734, 126735 (6), UU 3900-6; °8-14 km. N Miraflores Locks, TNHC 23374-88, 23390-409, 23411-38, 23440, 23442-60, 23462-76; 23478-83, 23492, 23555-60, 23562-76; °Río Chagres, AMNH 55430, 55439; °Río Cocolí, 3.5 km. N Miraflores Locks, TNHC 23410; °Summit, ANSP 23365-71, FMNH 22966-9, KU 97783-87. Chiriquí: 5.5 km. E Concepción, AMNH 69772; °14.4 km. E Concepción, AMNH 69773-8; 2 km. S David, AMNH 69779; °Progreso, UMMZ 58252, 58253 (2), 58254, 58436; Río Gariché, 8.3 km. ESE Paso Canoas, KU 103065-8. Coclé: 1 km. SE El Caño, KU 103042-51; El Valle de Antón, AMNH 59614-18 (10), 69785, ANSP 23502-5, KU 77201-14, MVZ 66578-83, UIMNH 46532. Colón: Cement Plant, Transisthmian Highway, FMNH 60394-5. Darién: El Real, KU 80454-5, 103052-64, UMMZ 125036 (10), USNM 140567-8; Río Canclon at Río Chucunaque, UMMZ 125035; °Río Chucunaque, near Yavisa, AMNH 59523. Los Santos: Tonosí, KU 101606-9. Panamá: 5 km. S Bejuco, AMNH 69782; 3 km. W Chepo, KU 77172-4, 104097-8 (tadpoles); °6 km. WSW Chepo, KU 77175; °Chico, Río La Jagua, USNM 129070; °La Joya, Cacora, ANSP 25129-33; Madden Dam, FMNH 67819; Nueva Gorgona, AMNH 69780-1; °1.6 km. W Nueva Gorgona, AMNH 69783-4; 1.5 km. W Pacora, 77176-200; °Río La Laja, near Chamé, ANSP 21845; °Río Tapia, MCZ 10048; °Tapia, AMNH 18930, 18950, 18952-3; °18 km. E Tocumen, MVZ 78662.

Colombia: Chocó: Sautatá, Atrato, FMNH 74918 (2), 74919. Magdalena: Aracataca, ANSP 19755-7; Curumani, MCZ 21465-74, UIMNH 28855; UMMZ 90168, USNM 118247; El Banco, Río Magdalena, ANSP 25061; Fundación, UMMZ 48281-2. Tolima: Espinal, MCZ 15068; Mariquita, FMNH 81822-3. Valle: Sevilla, MCZ 13751-3.

Hyla microcephala underwoodi Boulenger

Hyla microcephala Boulenger, Proc. Zool. Soc. London, p. 481, October 1, 1898 [Syntypes.—BMNH 94. 11. 1532-33 from Bebedero, Guanacaste Province, Costa Rica; C. F. Underwood collector] (not *Hyla microcephala* Cope, Proc. Amer. Philos. Soc., 23:281, February 11, 1886, from Chiriquí, Panamá).

Hyla underwoodi Boulenger, Ann. Mag. Nat. Hist., ser. 7, 3:277, April, 1899 (substitute name for *Hyla microcephala* Boulenger, preoccupied). Günther, Biologia-Centrali Americana, Reptilia and Batrachia, p. 278, September, 1901. Dunn and Emlen, Proc. Acad. Nat. Sci. Philadelphia, 84:25, March 22, 1932. Stuart, Misc. Publ. Mus. Zool., Univ. Michigan, 29:39, October 1, 1935. Taylor, Proc. Biol. Soc. Washington, 50:44, April 21, 1937. Stuart, Occas. Papers Mus. Zool., Univ. Michigan, 471:15, May 17, 1943. Taylor and Smith, Proc. U. S. Natl. Mus., 95:586, June 30, 1945. Stuart, Misc. Publ. Mus. Zool., Univ. Michigan, 69:35, June 12, 1948. Smith and Taylor, Bull. U. S. Natl. Mus., 194:85, June 17, 1948; Univ. Kansas Sci. Bull., 33:316, March 20, 1950. Stuart, Contr. Lab. Vert. Biol., Univ. Michigan, 45:48, May, 1950. Taylor, Univ. Kansas Sci. Bull., 35:891, July 1, 1952; Univ. Kansas Sci. Bull., 39:25, November 18, 1958.

Hyla phlebodes, Cole and Barbour, Bull. Mus. Comp. Zool., 50:154, November, 1906. Kellogg, Bull. U. S. Natl. Mus., 160:172, March 31, 1932.

Hyla microcephala martini Smith, Herpetologica, 7:187, December 31, 1951 [Holotype.—UIMNH 20965 from Encarnacion, Campeche, México; H. M. Smith collector]. Stuart, Contr. Lab. Vert. Biol., Univ. Michigan, 68:46, November, 1954. Fugler and Webb, Herpetologica, 13:105, July 10, 1957. Stuart, Contr. Lab. Vert. Biol., Univ. Michigan, 75:17, June, 1958. Neill and Allen, Publ. Research Div., Ross Allen's Reptile Inst., 2:26, November 10, 1959. Duellman, Univ. Kansas Publ., Mus. Nat. Hist., 13:62, August 16, 1960. Stuart, Herpetologica, 17:74, July 11, 1961. Hensley and Smith, Herpetologica, 18:70, April 9, 1962. Stuart, Misc. Publ. Mus. Zool., Univ. Michigan, 122:36, April 2, 1963. Holman and Birkenholz, Herpetologica, 19:144, July 3, 1963. Duellman, Univ. Kansas Publ., Mus. Nat. Hist., 15:225, October 4, 1963; Univ. Kansas Publ., Mus. Nat. Hist., 15:588, June 22, 1965.

Hyla microcephala underwoodi, Smith, Herpetologica, 7:188, December 31, 1951.

Diagnosis.—Brown lateral stripe narrow, extending to groin or only to sacral region, bordered above by narrow white line; dorsal pattern bold, consisting of X- or)(-shaped mark in scapular region or pair of interconnected dark lines on back; interorbital dark mark usually present; shanks usually having dark transverse bars.

Description and Variation.—The dorsal color pattern is highly variable. The various permutations of the X-shaped scapular mark and dark sacral marks differ proportionately in different samples. The variation in color pattern in 12 samples is summarized in Table 2. In samples from the southern part of the range (southern Nicaragua and Guanacaste Province, Costa Rica) more (40-93%) individuals have the lateral stripes extending to the groin than in northern samples (0-42%) from southern México and Guatemala. Likewise, the percentage of specimens lacking bars on the shanks and a dark interorbital bar is higher in the Costa Rican samples than elsewhere in the range. The

TABLE 2.—Variation in Color Pattern in Hyla microcephala underwoodi

POPULATION	N	Shanks		Inter-orbital bar		Dorso-lateral stripe		Scapular markings				Sacral markings		
		Bars	Flecks	Present	Absent	Groin	Sacrum	X	)(	||	Other	^	/\	Other
Oaxaca: Donají-Sarabia	27	22	5	27	0	0	27	23	4	0	0	7	6	14
Tabasco: Teapa-Villahermosa	55	46	9	55	0	0	55	53	2	0	0	19	11	23
Guatemala: La Libertad	51	51	0	51	0	17	34	45	6	0	0	16	14	21
Guatemala: Finca Chamá	32	32	0	32	0	0	32	32	0	0	0	26	2	4
Guatemala: Puerto Barrios	31	31	0	31	0	14	17	23	0	4	4	6	4	21
Honduras: Lago Yojoa	13	13	0	13	0	9	4	3	2	3	5	2	1	10
Nicaragua: La Cumplida	56	44	12	54	2	13	43	11	35	8	2	0	19	37
Nicaragua: Tipitapa	10	10	0	10	0	8	2	0	5	3	2	0	3	7
Nicaragua: Santo Thomás	10	10	0	10	0	8	2	3	0	7	0	0	5	5
Costa Rica: Tenorio-Tilarán	12	0	12	6	6	7	5	0	0	12	0	0	0	12
Costa Rica: Las Cañas-Liberia	38	21*	15	34	4	25	13	0	11	19	8	0	0	38
Costa Rica: Esparta	32	26	6	29	3	30	2	0	0	14	18	0	0	32

*Longitudinal stripes present in two specimens.

X- or)(-shaped scapular markings and /\- or / \-shaped sacral markings are most prevalent in northern samples, whereas to the south the dorsal markings are more commonly arranged in a pattern of paired lines, which usually are discontinuous and usually extend posteriorly only to the sacral region. Thus, the color pattern in *H. m. underwoodi* in the southern part of its range shows trends towards the pattern characteristic of *H. m. microcephala.* Intergrades between these two subspecies have been discussed in the account of the nominate subspecies.

When this frog is active at night its dorsum is pale yellow; faint flecks are present in some individuals. The white dorsolateral line usually is evident in the tympanic region, but in many individuals a dorsal pattern of lines and other marks is not evident. By day the dorsum changes to yellowish tan or pale brown with dark brown or reddish brown markings (Pl. 13). The venter is white, and the vocal sac in breeding males is yellow. The iris is pale bronze with a brown tint anterior and posterior to the pupil.

Remarks.—Hyla microcephala underwoodi has had a confused nomenclatural history. The taxon was first named *Hyla microcephala* by Boulenger (1898); this name was preoccupied by *Hyla microcephala* Cope (1886). Cole and Barbour (1906) and Kellogg (1932) used the name *Hyla phlebodes* Stejneger (1906) for specimens of this frog from México. Dunn (1931, 1933, 1934) applied the name *Hyla underwoodi* to Panamanian specimens that we identify as *Hyla phlebodes.* Smith (1951) named *Hyla microcephala martini* from southern México and Guatemala and considered the northern populations to represent a subspecies distinct from the Costa Rican *Hyla microcephala underwoodi,* despite the fact the Stuart (1935:39) stated that comparisons of specimens from El Petén, Guatemala, with the holotype of *Hyla underwoodi* showed only trivial differences.

Much of the confusion regarding the name *Hyla underwoodi* stems from the illustration given by Boulenger (1898:pl. 39, fig. 3) and reproduced by Taylor (1952:892), which shows a frog having a unicolor dorsum, dorsolateral white lines, and dark flanks. This pattern is in marked contrast to the pattern seen in most preserved specimens, which have the dorsum variously marked by dark brown lines or irregular marks. Smith (1951:185), in his description of *Hyla microcephala martini* from southern México, considered *H. underwoodi* to be a subspecies of *H. microcephala* that lacked dorsal dark markings.

Data accumulated in 1961 through field studies by the senior author at the type locality, Bebedero, and other localities in Guanacaste and Puntarenas provinces in Costa Rica provide a reasonable explanation of the differences in color pattern. As noted in the preceding description of this subspecies, at night the dorsal mark-

ings are not evident in many living individuals, whereas by day the dorsal markings are prominent. Most collectors prepare their specimens by day; consequently the majority of specimens have a pronounced dorsal pattern. Of the frogs collected in Costa Rica in 1961, some specimens were preserved at night; others from the same series were preserved by day. The differences are striking. In those preserved at night, dorsal markings are faint, if present at all. Some specimens closely match the figure given by Boulenger (1898).

It is extremely doubtful if the frog described and illustrated by Boulenger could be associated with either *Hyla phlebodes or H. microcephala microcephala*. Individuals of the former species lack a dorsolateral white line and always have some dorsal markings evident at night; furthermore, *H. phlebodes* is not known to occur on the Pacific lowlands. *Hyla microcephala microcephala* occurs farther southeast. Since there is no reason to doubt the type locality of *H. underwoodi*, since specimens from the area around the type locality that have been preserved at night are like the holotype in pattern, and since the characteristics of the populations of the frogs in Guanacaste are the same as, or gradually blend into those of, populations in northern Central America and southern México, the frogs from throughout the entire range can be referred to one taxon, the earliest name for which is *Hyla underwoodi* Boulenger, which herein is considered to be a subspecies of *H. microcephala* Cope.

Distribution.—*Hyla microcephala underwoodi* inhabits the Atlantic slopes and lowlands from southern Veracruz and extreme northern Oaxaca eastward across the base of the Yucatan Peninsula (possibly the species is extant in the northern part of the peninsula) to British Honduras and thence southeastward through the Caribbean lowlands and interior valleys in Honduras to central Nicaragua, where it apparently avoids the forested Caribbean lowlands and the dry Pacific lowlands of northwestern Nicaragua, but in the vicinity of Managua invades the Pacific lowlands and continues southward into northwestern Costa Rica as far as the Puntarenas Peninsula (Fig. 1). In México and Guatemala the species has not been taken at elevations of more than 350 meters, whereas farther south it occurs at higher elevations—780 meters at Silencio, Costa Rica, 830 meters on Montaña de Guaimaca, Honduras, 960 meters at Finca Tepeyac, Nicaragua, and 1200 meters at Finca Venecia, Nicaragua.

Specimens examined.—1270, as follows: **Mexico:** Campeche: Balchacaj, FMNH 100406, UIMNH 20944-6; Encarnación, FMNH 27069-70, 75784, MCZ 28360, 29637, UIMNH 20948-58, 20965, USNM 134264-5; Escárcega, UMMZ 122999; °7.5 km. W Escárcega, KU 71229-43; Laguna Alvarado, 65 km. S Xpujil, KU 75084-9; Pacaitún, Río Candelaria, FMNH 83118-20; °Tres Brazos, FMNH 113101-22, UIMNH 20947; 10 km. W Xpujil, KU 75082-3. Chiapas: Palenque, UIMNH 47984, 49139-50, USNM 114973-8. Oaxaca: °5 km. N Chiltepec, KU 87015-23; 3 km. N Donají UMMZ 115249 (9); °3.7 km. N Donají, UMMZ 115250 (5); °43 km. N Matías Romero, UIMNH 42550-68; °3.5 km. N Palomares, TNHC 25185, 25321-31, 25341-68; 4.6 km.

N Sarabia, UMMZ 115247 (2); °6.1 km. N Sarabia, UMMZ 115248 (11), °3 km. N Tolocita, KU 39655; Tuxtepec, KU 87024-40. TABASCO: 24 km. N Frontera, MCZ 35665-70; 0.8 km. E Río Tonolá, TNHC 25189; Teapa, UMMZ 119218 (4); °2.7 km. N Teapa, UMMZ 119216 (4); °10 km. N Teapa, UMMZ 119217 (6); °11.5 km. N Teapa, UMMZ 119219; °15.2 km. N Teapa, UMMZ 119220 (4); °17.6 km. N Teapa, UMMZ 119221 (12), 3.3 km. S Villahermosa, UMMZ 119215 (12), °17.6 km. S Villahermosa, UMMZ 119214 (12). VERACRUZ: 2.1 km. N Acayucan, UIMNH 42547-9; °6.4 km. NW Acayucan, UMMZ 115254 (14); 1.6 km. ESE Alvarado, UMMZ 115258 (39); °2.4 km. ESE Alvarado, UMMZ 115251 (2); °4.5 km. S Aquilera, UMZ 115252 (21); °8 km. SW Coatzacoalcos, UMMZ 119213 (10); 2.2 km. E Cosoleacaque, UMMZ 119222 (26); 10 km. SE Hueyapan, UMMZ 115255; 0.8 km. S Lerdo de Tejada, UMMZ 122778; °3.6 km. NE Minatitlán, TNHC 25150-2; 1.9 km. S Naranja, UMMZ 115253 (3); 4.5 km. NE Novillero, UMMZ 115256; San Andrés Tuxtla, FMNH 113124-8, UIMNH 20942-3. YUCATÁN: Chichén-Itzá, FMNH 36570, MCZ 2463 (2).

British Honduras: CAYO: 6.2 km. S El Cayo, MCZ 37885-92. STANN CREEK: Stann Creek, FMNH 49068.

Guatemala: ALTA VERAPAZ: 28.3 km. N Campur, KU 64578-90; Chinajá, KU 57425; Cubilquitz, UMMZ 90887, 90888 (4); Finca Chamá, UMMZ 90879 (13), 90880 (4), 90881, 90882 (28), 90883 (12), 90884 (46), 90885 (39), 90886 (20); °Finca Tinaja, BYU 16032; Panzós, UMMZ 90889 (2). CHIQUIMULA: Chiquimula, UMMZ 98113; 2 km. N Esquipulas, UMMZ 106844. EL PETÉN: La Libertad, KU 57447-97, 59907-11 (skeletons), MCZ 21461, UMMZ 75332 (13), 75333 (11), 75334 (14), 75335 (10); Piedras Negras, FMNH 113123, UIMNH 20966; °5 km. S Piedras Negras, USNM 114951-72; Tikal, UMMZ 117981 (2); Toocog, 15 km. SE La Libertad, KU 57426-46. EL QUICHÉ: Finca Tesoro, UMMZ 89165 (5). HUEHUETENANGO: Finca San Rafael, 16 km. SE Barillas, FMNH 40917-9. IZABAL: Puerto Barrios, FMNH 20004-7; 8 km. S Puerto Barrios, KU 57507-37, 59991 (eggs), 59992 (tadpoles); Quirigua, CAS 69657-701; 2.5 km. NE Río Blanco, KU 57539; San Felipe, FMNH 35065. ZACAPA: 14 km. ENE Mayuelas, KU 57502-6; 8 km. ENE Río Hondo, KU 57498-501.

Honduras: ATLANTIDAD: La Ceiba, UMMZ 91948 (2), USNM 117593-600; Lancetilla, MCZ 17981. CORTES: Lago Yojoa, AMNH 54917-9, 54957, 55134, KU 64563-77. EL PARAISO: Valle de Jamastran, AMNH 54807-12. FRANCISCO-MORAZAN: El Zamorano, AMNH 54873-81, KU 103223, UMMZ 123101; Montaña de Guaimaca, AMNH 54900-4 (8); Ranch San Diego, 19 km. SW Guaimaca, AMNH 53939. ITIBUCÁ: Vieja Itibucá, AMNH 54912-3.

Nicaragua: CHONTALES: 3 km. SW Santo Tomás, KU 64770-9, 68308 (skeleton). ESTELI: Finca Venecia, 7 km. N, 16 km. E Condega, KU 85296; 2.4 km. N Estelí, MCZ 28933-7. MANAGUA: 12-13 km. E Managua, KU 85297-301; °10 km. SW Tipitapa, UMMZ 119977 (10). MATAGALPA: °Finca Tepeyac, 10.5 km. N, 9 km. E Matagalpa, KU 85302-3; Hacienda La Cumplida, KU 64780-96, 68309-11 (skeletons), UMMZ 116482 (8), 116483 (23), 116484 (3), 116485 (5), 119984 (3). RIVAS: °Finca Amayo, 13 km. S, 14 km. E Rivas, KU 85304-7; 16 km. S Rivas, MCZ 29011-7; °20.5 km. SE Rivas, KU 85308-10; 5 km. SE San Pablo, KU 43111-4.

Costa Rica: GUANACASTE: Arenal, USC 6254 (2); °3 km. W Bagaces, USC 7019 (10); °3 km. NE Boca del Barranca, USC 8017 (21), °Finca San Bosco, USC 6272 (6), 6276 (3); °Guayabo de Bagaces, USC 7022 (4), 7023 (3), 7025; 12 km. S La Cruz, USC 8091 (2); °Laguna Arenal, USC 6262; °27 km. N Las Cañas, USC 8171 (6); °16 km. E Las Cañas, KU 102252-8; 16 km. SSE Las Cañas, KU 65090-5; °20 km. SE Las Cañas, KU 102251; Liberia, KU 36827-39; °7.3 km. N Liberia, USC 8096 (4); °10 km. N Liberia, USC 8085 (9); °7.5 km. SE Liberia, KU 65102-8, 68621-2 (skeletons); °14.7 km. S Liberia, USC 8238 (3); °4 km. W Liberia, KU 36847-57; 2 km. S Nicoya, USC 8230; °3-10 km. ESE Playa del Coco, USC 8012 (16), 8137 (14); °21.6 km. ESE Playa del Coco, USC 8138 (13); °Peñas Blancas, KU 102247-50; °Río Bebedero, 5 km. S Bebedero, KU 65089; °Río Higuerón, USC 7168 (2); Santa Cruz, USC 8232 (2); °Silencio, USC 6248; °Tenorio, KU 32313; Tilarán,

KU 36858-60; °2 km. E Tilarán, KU 86403, °5 km. NE Tilarán, KU 36840-6 USC 6269. Puntarenas: Barranca, KU 32305-12, °5 km. WNW Barranca, UMMZ 119976 (2); °10 km. E Esparta, KU 86400-2; 1 km. WNW Esparta, KU 65101; °4 km. WNW Esparta, KU 65088; °10 km. WNW Esparta, KU 65063-87, 68616-20 (skeletons); °12 km. WNW Esparta, KU 65096-100, USC 8251; 21.8 km. W San Ramón, USC 8242 (15).

Hyla robertmertensi Taylor

Hyla robertmertensi Taylor, Proc. Biol. Soc. Washington, 50:43, April 21, 1937 [Holotype.—CNHM 100096 (formerly EHT-HMS 2270) from Tapachula, Chiapas, México; H. M. Smith and E. H. Taylor collectors]. Smith and Taylor, Bull. U. S. Natl. Mus., 194:84, June 17, 1948; Univ. Kansas Sci. Bull., 33:326, March 20, 1950. Mertens. Senckenbergiana, 33:170, June 15, 1952; Senckenbergischen Naturf. Gesell., 487:30, December 1, 1952. Stuart, Contr. Lab. Vert. Biol., Univ. Michigan, 68:47, November, 1954. Duellman, Univ. Kansas Publ., Mus. Nat. Hist., 13:63, August 16, 1960. Duellman and Hoyt, Copeia, 1961 (2): 417, December 19, 1961. Porter, Herpetologica, 18:168, October 17, 1962. Stuart, Misc. Publ. Mus. Zool., Univ. Michigan, 122:36, April 2, 1963. Duellman and Trueb, Univ. Kansas Publ., Mus. Nat. Hist., 17:348, July 14, 1966.

Diganosis.—Brown lateral stripe wide, including loreal region and entire tympanum, extending to groin, bordered above by narrow white line; dorsum unicolor or with pair of dark lines (or rows of dashes) usually extending only to the sacral region; shanks having dark flecks, no transverse bars; interorbital bar lacking.

Description and Variation.—Males attain a maximum snout-vent length of 26.4 mm. in Oaxaca, whereas in a sample from Acacoyagua, Chiapas, the largest male has a snout-vent length of 25.7 mm., and from La Trinidad, Guatemala, 24-6 mm. Specimens from the western part of the range (eastern Oaxaca) have slightly smaller heads and proportionately larger tympani than the more eastern populations (Table 1).

The color pattern shows little variation, except in the nature of the dorsal markings. In a few specimens from throughout the range, but especially in the eastern part of the range, the dorsum lacks markings between the dorsolateral white lines. In most specimens the dorsal pattern consists of flecks or dashes arranged in two parallel longitudinal rows, and in some specimens the marks are fused into parallel lines. Small brown flecks are present on the dorsal surfaces of the shanks; in some specimens these flecks tend to form a longitudinal stripe on the shank. An interorbital dark mark is invariably absent.

When active at night *Hyla robertmertensi* is pale yellow above with a white dorsolateral line and pale brown lateral stripe; the dorsal markings are faint. By day the dorsum is yellowish tan with brown markings. The dorsolateral stripe is creamy white, and the lateral stripe is dark brown (Pl. 14). The venter is white, and the iris is dull bronze. In breeding males the vocal sac is yellow.

Remarks.—Although this species superficially resembles *Hyla microcephala microcephala,* the latter is easily distinguished by the narrow brown lateral stripe, as compared with the much wider stripe in *H. robertmertensi.* No other hylids in northern Central America and southern México can be confused with this species.

Distribution.—*Hyla robertmertensi* inhabits the Pacific slopes (to elevations of 700 meters) and lowlands from eastern Oaxaca (east of the Plains of Tehuan-

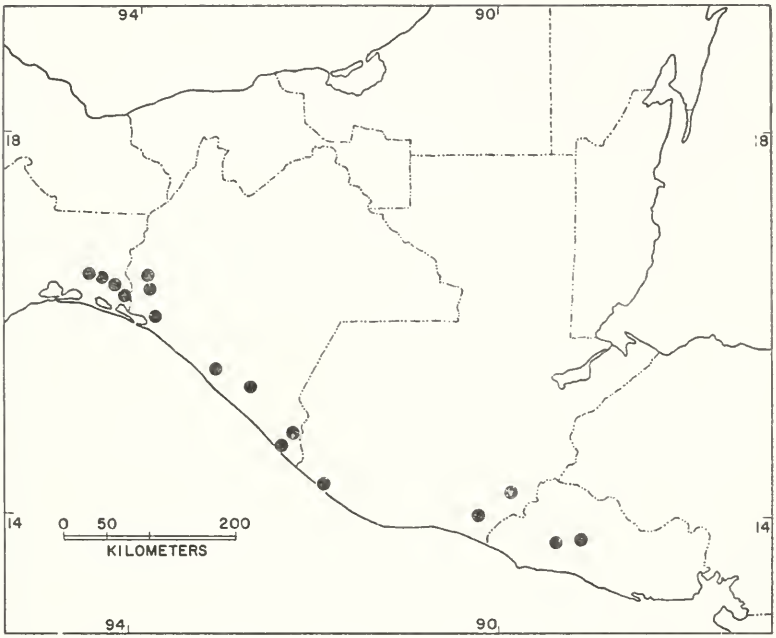


FIG. 2. Map showing locality records for *Hyla robertmertensi.*

tepec) southeastward to central El Salvador. The species also occurs in the Cintalapa Valley (Atlantic drainage) in southwestern Chiapas (Fig. 2.) The distribution seems to be limited on the northwest and southeast by arid environments. The region in which *Hyla robertmertensi* lives is characterized by higher rainfall and more luxuriant vegetation than occur on the Plains of Tehuantepec or on the Pacific lowlands of eastern El Salvador and southern Honduras. In addition to the localities listed below, Mertens (1952:30) recorded the species from Hacienda Cuyan-Cuya, Depto. Sonsonate, El Salvador.

Specimens examined.—490, as follows: **Mexico:** CHIAPAS: Acacoyagua, USNM 114754-61; °2 km. W Acacoyagua, UMMZ 87843 (28), 87844 (50), 87845 (50), 87846 (45), 87847 (27), 87848 (3); 32 km. N Arriaga, KU 57619-24, 59917-8 (skeletons); Asunción, FMNH 100413, 100501-4, UIMNH 26989-90, USNM 134267; °La Esperanza, USNM 114737-48, 114750-3, 17 km. S Las Cruces, KU 57625-49, 59997 (eggs); 8.5 km. N Puerto Madero, UMMZ 119981 (2); °11.7 km. N Puerto Madero, UMMZ 119982; Tapachula, FMNH 100096, UIMNH 26987; °11 km. S Tapachula, KU 57605-18, 59916 (skeleton); Tonolá, FMNH 27073, 100505-10, UIMNH 26988. OAXACA: Tapanatepec, UMMZ 115245 (2), °1.6 km. E Tapanatepec, UMMZ 115244 (14); °4.3 km. E Tapanatepec, UIMNH 38368-9; °7.5 km. W Tapanatepec, UMMZ 115246 (39); 12.8 km. W Tapanatepec, KU 65007-14; 7.2 km. WNW Zanatepec, UMMZ 115243 (77); °13.6 km. WNW Zanatepec, TNHC 25213-22; 22.7 km. WNW Zanatepec, TNHC 25203-9.

Guatemala: JUTIAPA: Jutiapa, UMMZ 106848; La Trinidad, UMMZ 107733 (23). RETALHUELEU: Casa Blanca, UMMZ 107732.

El Salvador: LA LIBERTAD: 16 km. NW Santa Tecla, KU 44112. SAN SALVADOR: 21.9 km. N San Salvador, UMMZ 119983 (6).

Hyla phlebodes Stejneger

Hyla phlebodes Stejneger, Proc. U. S. Natl. Mus., 30:817, June 4, 1906 [Holotype.—USNM 2997 from "San Carlos," Costa Rica; Burgdorf and Schild collectors]. Taylor, Proc. Biol. Soc. Washington, 50:44, April 21, 1937; Univ. Kansas Sci. Bull., 35:888, July 1, 1952; Univ. Kansas Sci. Bull., 39:25, November 18, 1958. Fouquette, Evolution, 14:484, December 16, 1960. Duellman and Trueb, Univ. Kansas Publ., Mus. Nat. Hist., 17:348, July 14, 1966.

Hyla underwoodi, Dunn, Occas. Papers Boston Soc. Nat. Hist., 5:413, October 10, 1931; Occas. Papers Boston Soc. Nat. Hist. 8:72, June 7, 1933; Amer. Mus. Novitiates, 747.2, September 17, 1934, Gaige, Hartweg, and Stuart, Occas. Papers Mus. Zool., Univ. Michigan, 357:5, October 26, 1937. Breder, 1946, Bull. Amer. Mus. Nat. Hist., 86:416, August 22, 1946.

Diagnosis.—Dark brown lateral stripe, if present, usually extending only to insertion of forearm, never posteriorly to sacral region; white line above brown stripe absent or faint; dorsal pattern weak, usually consisting of irregular dashes or interconnected lines; interorbital dark mark present; shanks having weakly defined transverse bars.

Description and variation.—In the majority of specimens (70%) the lateral dark stripe extends from the nostril to the eye and thence above the tympanum to a point above the insertion of the arm; in 17 per cent the stripe extends to the mid-flank, whereas in 13 per cent the stripe is absent. A narrow and faint white line is present on the canthus in some specimens, but no distinct white stripe is present above the lateral dark line posterior to the eye. An interorbital bar and transverse marks on the shanks are invariably present. The dorsal markings are variable, but in most specimens (92%) consist of either an X- or)(-shaped mark in the scapular region; in the other specimens the markings are irregular short lines or absent. Approximately equal numbers of specimens have a transverse bar, chevron, or broken lines in the sacral region, whereas about eight per cent of the specimens lack markings in the sacral region.

When active at night, individuals are pale yellowish tan with faint brown dorsal markings. By day they are tan with more distinct brown markings (Pl. 14). The thighs are pale yellow; the belly is white. The iris is pale creamy tan with brown flecks. In breeding males the vocal sac is yellow.

Tadpoles.—Tadpoles of this species have been found in an extensive grassy pond at Puerto Viejo, Costa Rica. The following description is based on KU 104099, a specimen in development stage 36 (Gosner, 1960).

Total length, 21.0 mm.; body length, 6.7 mm.; body slightly wider than deep, snout pointed; nostrils large, directed anteriorly, situated near end of snout; eyes small, situated dorsolaterally, directed laterally; spiracle sinistral, located just posteroventral to eye; anal tube dextral. Tail xiphicercal; caudal musculature moderately deep, extending far beyond posterior edge of fins; fins deepest at about midlength; dorsal fin extending onto body, slightly deeper than caudal musculature; ventral fin slightly shallower than musculature. Mouth small, terminal, lacking teeth and fringing papillae, but having finely serrate beaks. In preservative top of head olive-tan with brown flecks; dark stripe from snout through eye to posterior edge of body; belly white, flecked with brown anteriorly; tail creamy tan with grayish brown blotches. In life, dorsum of body reddish tan mottled with darker brown; lateral stripe dark brown; belly white, mottled with brown and black; caudal musculature heavily pigmented

with grayish tan; posterior tip of tail marked with dark gray; caudal fins heavily blotched with grayish tan; iris orange-tan peripherally, red centrally (Pl. 15).

Remarks.—This species has been confused with *Hyla microcephala underwoodi* by many workers. Dunn (1931, 1933, 1934) and Breder (1946) referred Panamanian specimens of *H. phlebodes* to *H. underwoodi;* likewise, Gaige, Hartweg, and Stuart (1937) made the same error. Cole and Barbour (1906) and Kellog (1932) used the name *H. phlebodes* for Mexican specimens of *H. microcephala underwoodi.* The similarity in color pattern of *H. microcephala underwoodi* and *H. phlebodes* easily accounts for the misapplication of names. Although both species have nearly identical dorsal color patterns, that of *H. microcephala underwoodi* usually is bolder. Furthermore, in that species a narrow white line usually is present above the well-defined lateral dark stripe, whereas the lateral dark stripe is short and posterior to the eye is not bordered above by a white line in *H. phlebodes.*

The type locality "San Carlos, Costa Rica" given by Stejneger (1906:817) apparently refers to a region, the Llanuras de San Carlos, in the northern part of Alajuela Province, Costa Rica.

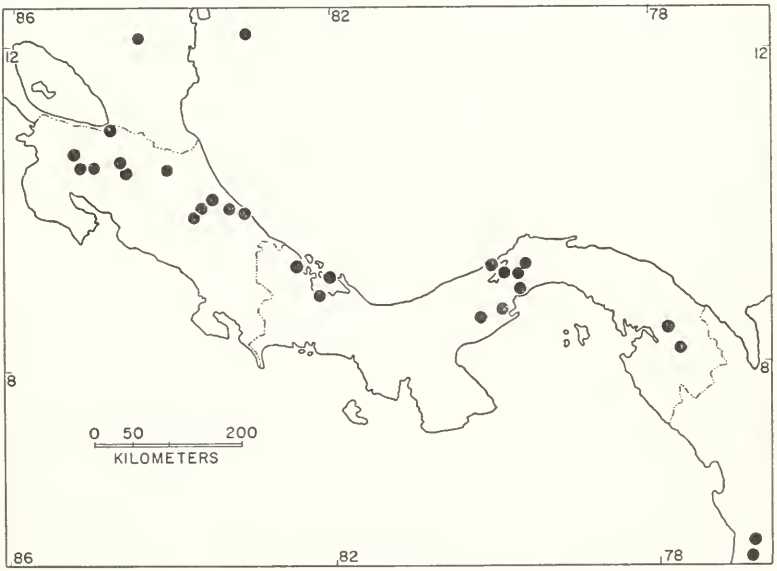


FIG. 3. Map showing locality records for *Hyla phlebodes.*

Distribution.—Hyla phlebodes inhabits humid tropical forests from southeastern Nicaragua southeastward on the Caribbean slopes and lowlands to the Canal Zone in Panamá, thence eastward in the Chucunaque Basin of eastern Panamá and onto the Pacific lowlands of Colombia (Fig. 3). The species also

reaches the Pacific slopes in the Arenal Depression in northwestern Costa Rica and in the Panamanian isthmus, where it occurs in humid forests on the Pacific slope of El Valle and Cerro La Campana. Mostly the species is found at low elevations, but it occurs at 600 meters at Turrialba and at 700 meters at Finca San Bosco in Costa Rica.

Specimens examined.—410, as follows: Nicaragua: Zelaya: Isla Grande del Maíz, MCZ 14848; Río Mico, El Recrero, UMMZ 79720 (6).

Costa Rica: Alajuela: 12.4 km. N Florencia, MVZ 76108-10, USC 2628; *Las Playuelas, 11 km. S Los Chiles, USC 7216; Los Chiles, USC 7217, 7219; 3 km. NE Muelle de Arenal, USC 2644 (2); *"San Carlos," USNM 29970. Cartago: Chitaría, KU 103690; *1.6 km. E Río Reventazón Bridge, east of Turrialba, UMMZ 119978 (2); *Tunnel Camp, near Peralta, KU 32456, 32458-69, 41098 (skeleton); Turrialba, FMNH 101794, 103188-9, KU 25725-9, 32439-48, 41095-7 (skeletons), 64797-827, 68300-2 (skeletons), 68403 (eggs), 68404 (tadpoles), MCZ 29224-5, 29310-2, UMMZ 119979 (6), USC 31, 256 (2), 458 (2), 580, 594, 599 (7), 7074 (2), USNM 29933. Guanacaste: Arenal, USC 6254; *Finca San Bosco, USC 62724), 6276 (3), Guayabo de Bagaces, USC 7022 (3), 7023; *Laguna Arenal, USC 6262 (4); 3 km. NE Tilarán, USC 524; *5 km. NE Tilarán, USC 6269; *6 km. NE Tilarán, UMMZ 122653 (6), S-2680 (skeleton), USC 523 (8). Heredia: Puerto Viejo, KU 64828-63, 68303-7 (skeletons), 68405-6 (tadpoles), 104099-100 (tadpoles); *1.5 km. N Puerto Viejo, KU 64871; *1 km. S Puerto Viejo, KU 86432-40; *4.2 km. W Puerto Viejo, KU 64864-5; *5.9 km. W Puerto Viejo, KU 64866-70; *7.5 km. W Puerto Viejo, KU 86431. Limón: Batán, UMMZ 119980 (2); La Castilla, ANSP 23707; Puerto Limón, KU 32449-55.

Panama: Bocas del Toro: 3.2 km. NW Almirante, KU 96026; Cayo de Agua, KU 96027-31; Fish Creek, KU 96032-4. Canal Zone: Barro Colorado Island, AMNH 69790, ANSP 23244-50; FMNH 13380, 22972-4; Juan Mina, AMNH 55429, UU 3899; *8.6-13.8 km. N Miraflores Locks, TNHC 23439, 23477, 23484-8, 23491, 23494-9, 23501-2, 23504-8, 23510-17, 23519-30, 23532-8, 23541-54, 23561. *Río Chagres, AMNH 55431-4; Río Cocolí, 3.5 km. N Miraflores Locks, TNHC 23461, 23489-90, 23493, 23500, 23503, 23509, 23518, 23531, 23539-40; *Summit, ANSP 23361, KU 97788; *Three Rivers Plantation, SU 2130. Coclé: El Valle de Antón, AMNH 55435, 69786-9, ANSP 23506-9. Colón: Achiote, KU 77215-78; Ciricito, CAS 71499-500, 71505-6. Darién: Río Canclon at Río Chucunaque, UMMZ 126733; Río Chucunaque, near Yavisa, AMNH 51783. Panamá: Cero La Campana, FMNH 67847-50.

Colombia: Chocó: Andagoya, FMNH 81856; Boca de Raspadura, AMNH 13570-8.

Hyla sartori Smith

Hyla underwoodi (in part), Smith and Taylor, Bull. U. S. Natl. Mus., 194:85, June 17, 1948.

Hyla microcephala sartori Smith, Herpetologica, 7:186, December 31, 1951 [Holotype.—UIMNH 20934 from 1 mile north of Organos, south of El Treinte, Guerrero, México; H. M. Smith and E. H. Taylor collectors]. Duellman, Univ. Kansas Publ., Mus. Nat. Hist., 15:124, December 20, 1961. Porter, Herpetologica, 18:168, October 17, 1962. Davis and Dixon, Herpetologica, 20:230, January 25, 1965. Duellman, Univ. Kansas Publ. Mus. Nat. Hist., 15:652, December 30, 1965.

Diagnosis.—Dorsum tan with broad dark brown chevrons or transverse bars; shanks marked with two or three broad transverse bars; dorsolateral stripes absent.

Description and variation.—No noticeable geographic variation is apparent in either structural features or coloration in this species. All specimens lack a dorsolateral dark stripe and white line, although a dark line is present on the

canthus and dissipates in the loreal region. A broad interorbital brown bar is present in all specimens. The color pattern on the dorsum invariably consists of a broad, dark, chevron-shaped mark in the scapular region and a broad dark chevron or transverse bar in the sacral region. The shanks invariably have two or three dark brown transverse bars.

When active at night individuals are yellowish tan above with chocolate brown markings (Pl. 14). The belly is white, and the thighs are pale yellowish tan. The iris is dark bronze-color. In breeding males the vocal sac is yellow. By day some individuals were observed to change to creamy gray with distinct darker markings.

Remarks.—Although tadpoles of this species have not been found, observations on the breeding sites indicate that the tadpoles probably develop in ponds. Except for calling males observed around a pool in a stream-bed 11.8 kilometers west-northwest of Tierra Colorada, Guerrero, all breeding congregations have been found at temporary ponds.

Smith (1951:186) named *Hyla sartori* as a subspecies *of Hyla microcephala.* This subspecific relationship seemed reasonable until analysis of the mating calls showed that the call of *H. sartori* is more nearly like that of *H. phlebodes* than that of *H. microcephala.* The broad hiatus separating the ranges of *H. microcephala* and *H. sartori* is additional evidence for considering *H. sartori* as a distinct species.

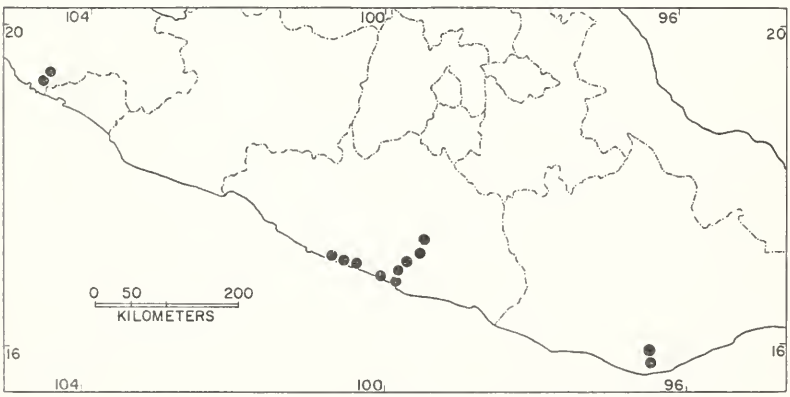


FIG. 4. Map showing locality records for *Hyla sartori.*

Distribution.—*Hyla sartori* occurs in mesophytic forests to elevations of about 300 meters on the Pacific slopes of southern México from southwestern Jalisco to south-central Oaxaca (Fig. 4). The lack of specimens from Colima and Michoacán probably reflects inadequate collecting instead of the absence of the species there. On the basis of available habitat the species would be expected to occur in Nayarit, but extensive collecting there has failed to reveal its presence. The semi-arid Plains of Tehuantepec apparently limit the distribution to the east.

Specimens examined.—190, as follows: México: Guerrero: 5 km. E Acapulco, AMNH 54611-2; 23.2 km. N Acapulco, UIMNH 26404-7; Colonia Buenas Aires, 23 km. E Tecpán de Galeana, UMMZ 119223 (7); *El Limoncito, FMNH 75785, 100390-402, 104631, 104633, UMMZ 117250, USNM 134266; El Treinte, FMNH 100403, UIMNH 20935-7; Laguna Coyuca, AMNH 59686; La Venta, MCZ 29635; * Morjonares, UIMNH 26392-402; 1.6 km. N Organos, FMNH 100404-5, UIMNH 20933-4; 19.2 km. S Petaquillas, UIMNH 26408; 6.1 km. E. Tecpán de Galeana, TNHC 23396-408; * 11.2 km. N Tierra Colorada, UIMNH 26403; 11.8 km. WNW Tierra Colorada, UMMZ 119225 (51), S-2677-9 (skeletons); Zacualpán, UMMZ 119224 (6). Jalisco: 6.4 km. NE La Resolana, KU 67853-69; 24 km NE La Resolana, KU 67870-3. Oaxaca: 3 km. N Pochutla, KU 57539; 13.4 km. N Pochutla, UMMZ 123495 (40).

CRANIAL OSTEOLOGY

The frogs of the *Hyla microcephala* group have a minimal amount of cranial ossification as compared to more generalized hylid skulls, such as *Smilisca* (Duellman and Trueb, 1966). In the *Hyla microcephala* group the sphenethmoid is small and short, and a large frontoparietal fontanelle is present. The quadratojugal exists only as a small spur and is not in contact with the maxillary. The proötics are poorly developed. The anterior and posterior arms of the squamosal are short; the anterior arm extends no more than one-fourth of the distance to the maxillary, and the posterior arm does not have a bony connection with the proötic. The nasal lacks a maxillary process, and the medial ramus of the pterygoid lacks a bony connection to the proötic.

Teeth are absent on the parasphenoid and palatines, but present on the maxillaries, premaxillaries, and prevomers. The teeth are simple, pointed, and slightly curved. Although the number of teeth varies (Table 3), no consistent differences between the species are apparent.

Table 3.—Variation in the Number of Teeth in the Species of the Hyla Microcephala Group. (N=Number of Jaws, or Twice the Number of Individuals; Means are Given in Parentheses After the Observed Ranges).

Species	N	Maxillary	Premaxillary	Prevomer
H. microcephala	32	31–47 (37.8)	4–13 (8.9)	2–4 (3.2)
H. phlebodes	10	38–45 (40.1)	8–13 (10.3)	2–5 (3.9)
H. robertmertensi	6	23–43 (32.8)	7–12 (10.5)	2–3 (2.7)
H. sartori	6	27–43 (38.2)	9–10 (9.3)	3–4 (3.7)

Despite the great reduction in the ossification of the cranial elements, certain apparently consistent differences exist between

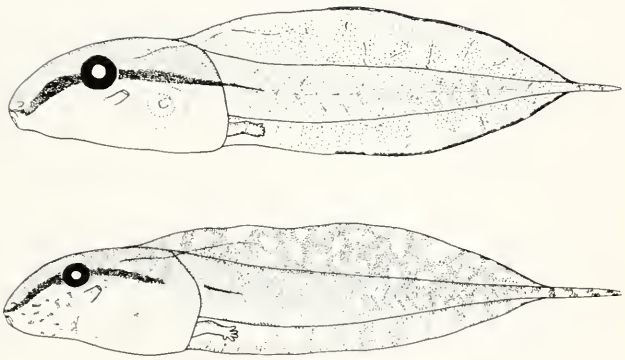
PLATE 13

Upper figure, *Hyla microcephala microcephala* (KU 64593); middle figure, *H. microcephala underwoodi* (KU 64565); lower figure, *H. microcephala underwoodi* (UMMZ 115247). All approximately $\times 3$.

PLATE 14

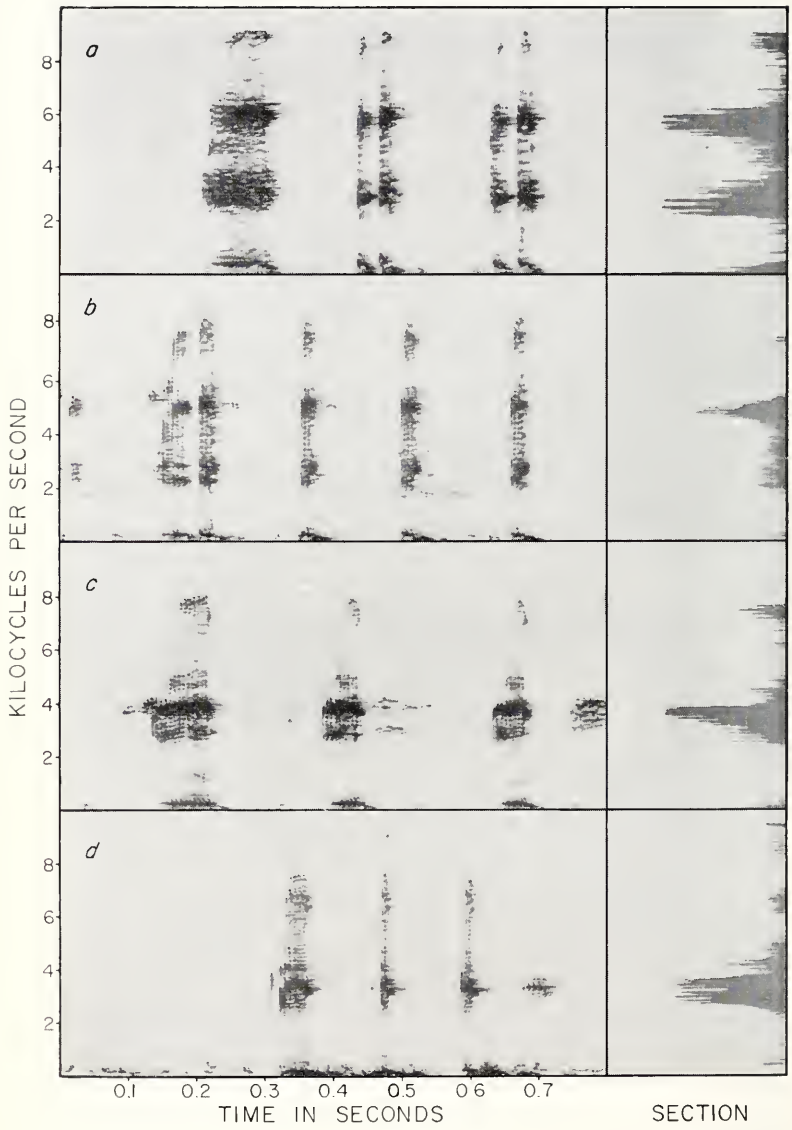
Upper figure, *Hyla robertmertensi* (UMMZ 115243); middle figure, *H. phlebodes* (KU 64798); lower figure, *H. sartori* (UMMZ 119225). All approximately × 3.

PLATE 15



Tadpoles of *Hyla microcephala* group: upper figure, *H. m. microcephala* (KU 104097); lower figure, *H. phlebodes* (KU 104099). Both × 4.

PLATE 16



Audiospectrograms and sections of mating calls of *Hyla microcephala* group: (a) *H. m. microcephala* (KU Tape No. 19); (b) *H. robertmertensi* (KU Tape No. 41); (c) *H. phlebodes* (KU Tape No. 6); (d) *H. sartori* (KU Tape No. 190).

TABLE 4.—Comparative Cranial Osteology of Hyla microcephala Group

CHARACTER	*H. microcephala*	*H. robertmertensi*	*H. phlebodes*	*H. sartori*
Frontoparietal.....	Minimally ossified with large fontanelle extending from sphenethmoid to occipital ridge.	Ossification extensive anteriorly with narrow medial separation; fontanelle largest in parietal region.	Ossification extensive anteriorly with narrow medial separation; fontanelle largest in parietal region.	Ossification moderately extensive anteriorly; medial separation of about uniform width throughout length of fontanelle.
Nasals.....	Moderately long and slender; arcuate in dorsal view.	Moderate in size; slightly wider anteriorly than posteriorly in dorsal view.	Moderate in size; slightly wider anteriorly than posteriorly in dorsal view.	Long and broad; arcuate in dorsal view.
Sphenethmoid.....	Extremely short in dorsal view.	Moderately short in dorsal view.	Moderately short in dorsal view.	Moderately short in dorsal view; ossified anteriorly between nasals.
Columella.....	Distal end greatly expanded.	Distal end slightly expanded or not.	Distal end not expanded.	Distal end not expanded.

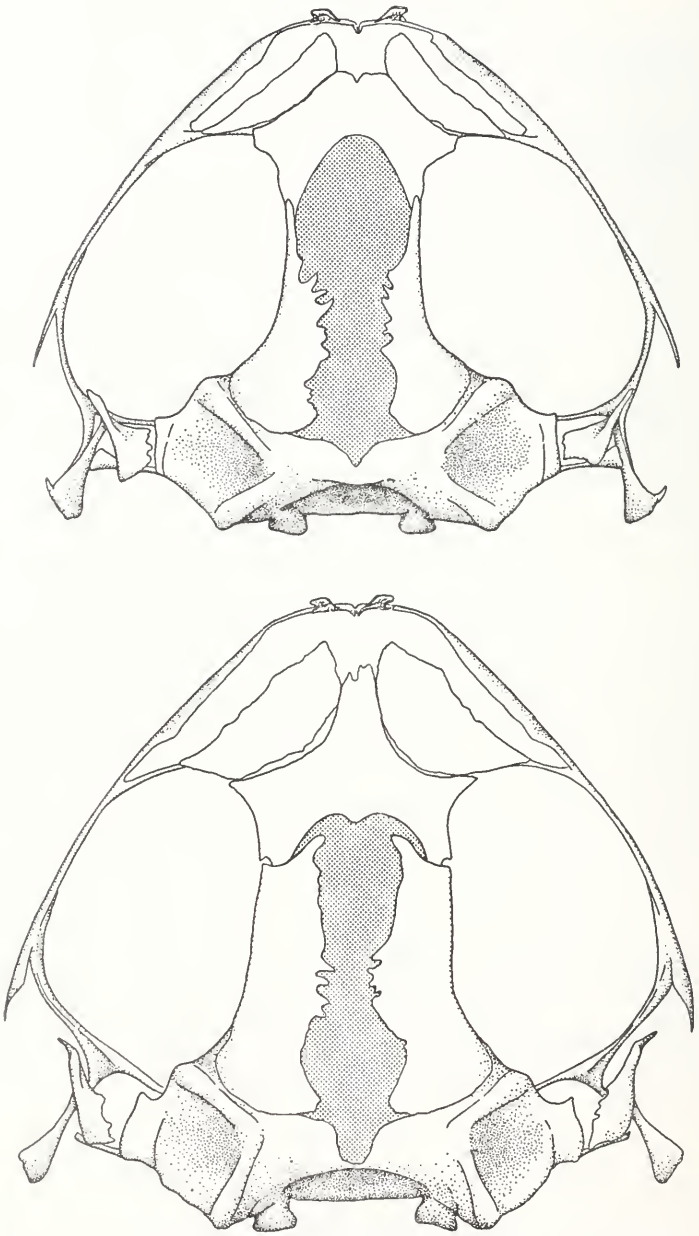


FIG. 5. Dorsal views of the skulls of (a) *Hyla m. microcephala* (KU 68293) and (b) *H. sartori* (UMMZ S-2677). Both × 12.

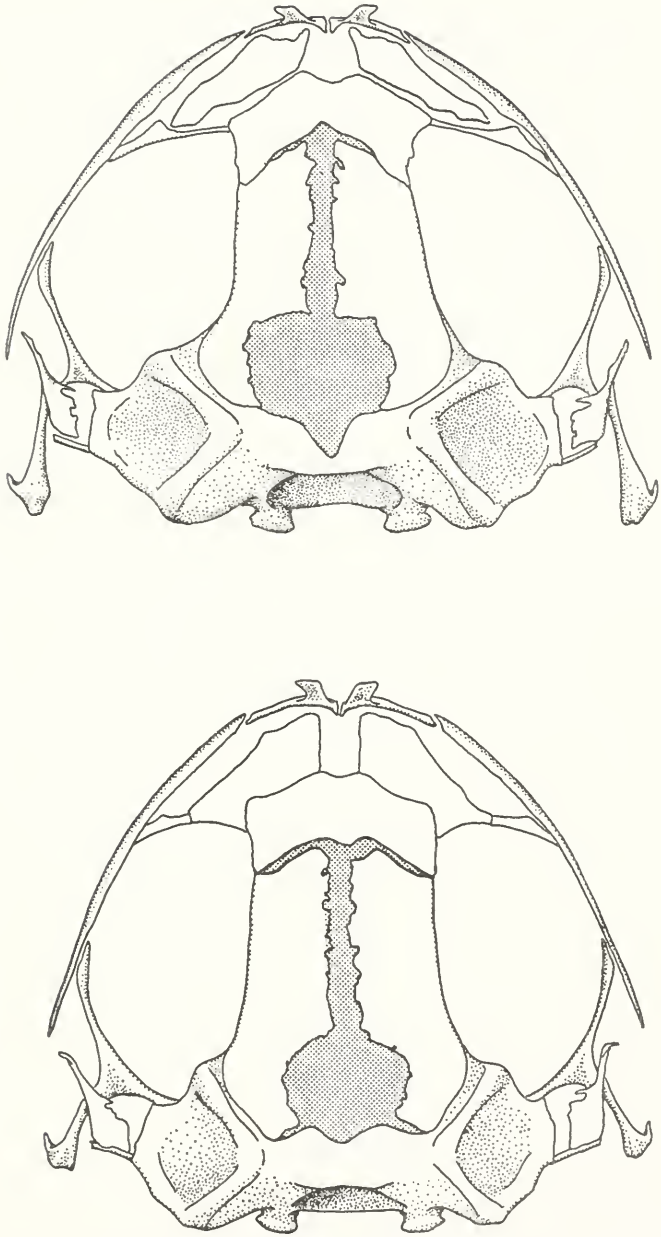


FIG. 6. Dorsal views of skulls of (a) *Hyla phlebodes* (KU 68303) and (b) *H. robertmertensi* (KU 59917). Both × 12.

the species seem to be consistent. The most notable differences are: 1) amount of ossification of the frontoparietals and consequent shape and size of the frontoparietal fontanelle, 2) shape of the nasals, 3) shape and extent of the sphenethmoid, and 4) shape of the columella (Table 4, Figs. 5-6). On the basis of these characters, *Hyla microcephala* can be set apart from the other species and characterized as having a poorly ossified frontoparietal and correspondingly large frontoparietal fontanells; long, slender, arcuate nasals; extremely short sphenethmoid; and expanded distal end of the columella. The other species in the group (*phlebodes, robertmertensi,* and *sartori*) have more ossification of the frontoparietals, broader nasals, only a moderately short sphenethmoid, and an unexpanded distal end of the columella. Among these three species, the skulls of *phlebodes* and *robertmertensi* are most nearly alike, whereas the skull of *sartori* differs by having a differently shaped frontoparietal fontanelle, broader nasals, and an ossified anterior extension of the sphenethmoid between the nasals (compare Fig. 5b with Fig. 6 a-b).

Although all skulls examined belong to breeding adults, the extent of the ossification of the frontoparietals and the resulting shape of the frontoparietal fontanelle might be correlated with the age of the frog. Nevertheless, in the 24 skulls of *Hyla microcephala* examined, the frontoparietals are less extensively ossified than in the skulls of the other species. The trivial differences among the other three species certainly are suggestive of close relationship, but on the basis of present knowledge of the evolutionary trends in hylid cranial osteology, the differences offer little evidence for determining phylogenetic lineage.

ANALYSIS OF MATING CALLS

Calls of all five taxa were compared in several characteristics, of which three are deemed most significant systematically. These are 1) the pattern and duration of the notes of a call-group, 2) the fundamental frequency, and 3) the dominant frequency. Air temperatures were noted at the time the calls were recorded, but no valid correlation could be determined between this factor and any of the parameters of the calls; consequently recordings made at all temperatures (21-29° C.) were grouped together.

Pattern and duration of notes.—In all five taxa the basic pattern consists of a call-group made up of one primary note followed by a series of shorter secondary notes. In some species the secondary

notes differ from the primary in other characteristics. Both subspecies of *Hyla microcephala* have a long, unpaired primary note followed by 0 to 18 (usually about 4) somewhat shorter paired secondary notes. In calls of *Hyla m. microcephala* the mean duration of the primary is 0.131 (0.10-0.16) second and that of the secondaries is 0.101 (0.05-0.14) second, whereas in *H. m. underwoodi* the mean duration of the primary is 0.018 (0.05-0.15) second and that of the secondaries is 0.086 (0.06-0.11) second.

Hyla robertmertensi has a reverse of this pattern in that the primary note is paired and the secondaries are unpaired. In the sample studied a call-group contains 0-28 secondary notes (generally about 3). The mean duration of the primary is 0.091 (0.07-0.11) second and that of the secondaries is 0.040 (0.025-0.06) second.

Hyla phlebodes and *sartori* have call-groups composed of a rather short, unpaired primary and several short, unpaired secondaries (0-28 in *phlebodes,* 0-23 in *sartori*). The mean duration of the primary of *phlebodes* is 0.105 (0.07-0.16) second and that of the secondaries is 0.067 (0.035-0.12) second. The mean duration of the primary of *sartori* is 0.080 (0.07-0.09) second and that of the secondaries is 0.053 (0.035-0.07) second.

The two subspecies of *H. microcephala* are identical in call pattern and agree closely in duration of notes, although those of the nominate subspecies tend to be slightly longer. *Hyla robertmertensi* is distinctive in call pattern in that it is the only species having a paired primary; the duration of the primary is completely overlapped by that in the other species, but the secondaries tend to be the shortest in the group. The call patterns of *H. phlebodes* and *H. sartori* are identical and the range of duration of notes of *phlebodes* completely overlaps that of *sartori,* although both the primary and secondary notes of the latter tend to be somewhat shorter (Table 5, Pl. 16).

Fundamental frequency.—This parameter was analyzed for the primary notes. It was measured for the secondaries as well and was found to differ in magnitude in the same way as the primary note. In a few examples of both subspecies of *H. microcephala* a high prrimary note, in which the fundamental frequency is exceptionally high, is sometimes emitted (Fouquette, 1960b). None of these notes was used in this analysis; only the fundamental frequencies of normal primary notes are compared (Table 5, Fig. 7).

The two subspecies of *H. microcephala* agree closely in fundamental frequency. There is considerable overlap, but the difference between the means is significant at the 0.001 level of probability ($t = 4.2406$). The call of *H. robertmertensi* does not overlap that

TABLE 5.—Comparison of Normal Mating Calls in the Hyla microcephala Group. (Observed Range Given in Parentheses Below Mean; Unless Otherwise Noted Data Are for Primary Notes.)

SPECIES	N	Dominant frequency (cps)	Fundamental frequency (cps)	Duration of notes (seconds)		Repetition rate of secondaries (notes/minute)
				Primary	Secondary	
H. m. microcephala	44	5637 (5150–5962)	205 (184–244)	0.13 (0.11–0.16)	0.10 (0.05–0.14)	268 (192–353)
H. m. underwoodi	47	5772 (5177–6200)	220 (192–275)	0.11 (0.05–0.15)	0.09 (0.06–0.11)	283 (197–384)
H. robertmertensi	25	5388 (5150–5785)	162 (140–178)	0.09 (0.07–0.11)	0.04 (0.03–0.06)	418 (368–570)
H. phlebodes	34	3578 (3220–4067)	148 (125–158)	0.11 (0.07–0.16)	0.07 (0.04–0.12)	284 (210–350)
H. sartori	10	3217 (2950–3600)	126 (116–135)	0.08 (0.07–0.09)	0.05 (0.04–0.07)	434 (396–477)

of *H. sartori* or either subspecies of *H. microcephala* in this parameter; but it does overlap that of *H. phlebodes,* although again the difference between the means is significant at the 0.001 level ($t = 9.360$). *Hyla phlebodes* and *sartori* have the lowest fundamental frequencies, and there is some overlap, but here too the difference between the means is significant at the 0.001 level ($t = 4.923$).

Dominant frequency.—A dominant band of of frequencies cuts across the harmonics of the fundamental, obscuring the harmonic pattern and generally shifting upward in frequency. The midpoint of this band is measured at the terminal border as the dominant frequency. As with the fundamental frequency, only the normal primary notes were utilized in the comparisons (Table 5, Fig 8).

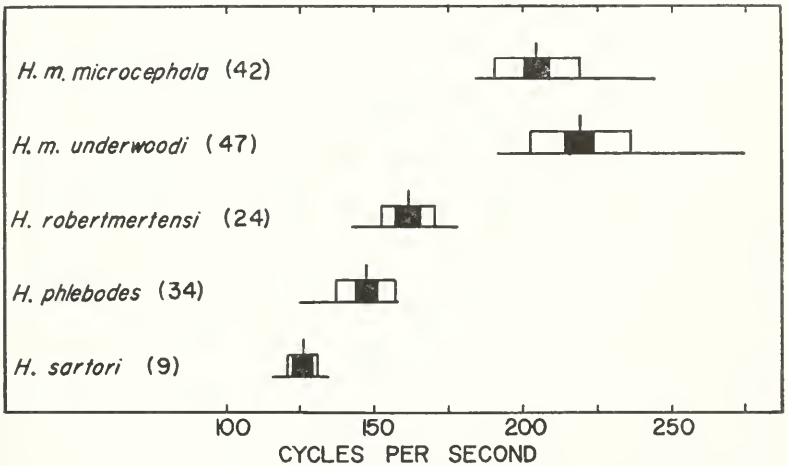


FIG. 7. Variation in the fundamental frequency of the normal primary notes in the *Hyla microcephala* group. The horizontal lines = range of variation, vertical lines = mean, solid bars = twice the standard error of the mean, and open bars = one standard deviation. The number of specimens in each sample is indicated in parentheses after the name of the taxon.

The two subspecies of *H. microcephala* agree more closely in this parameter than in fundamental frequency. The overlap is great, but the difference between the means is significant at the 0.001 level ($t = 3.658$). The calls of both subspecies completely overlap that of *robertmertensi* in this parameter, but the difference between the means is significant at the 0.001 level. The calls of *H. phlebodes* and *H. sartori* overlap considerably in this characteristic, although the difference between the means is significant at the 0.001 level ($t = 7.504$) (Fig. 9). The call of neither species overlaps those of *H. microcephala* and *robertmertensi.*

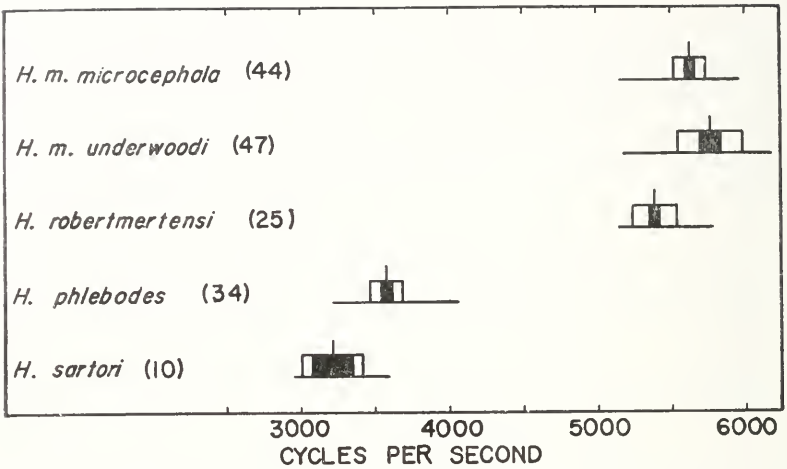


FIG. 8. Variation in the mid-point of the dominant frequency band of the normal primary notes in the *Hyla microcephala* group. The horizontal lines = range of variation, vertical lines = mean, solid bars = twice the standard error of the mean, and open bars = one standard deviation. The number of specimens in each sample is indicated in parentheses after the name of the taxon.

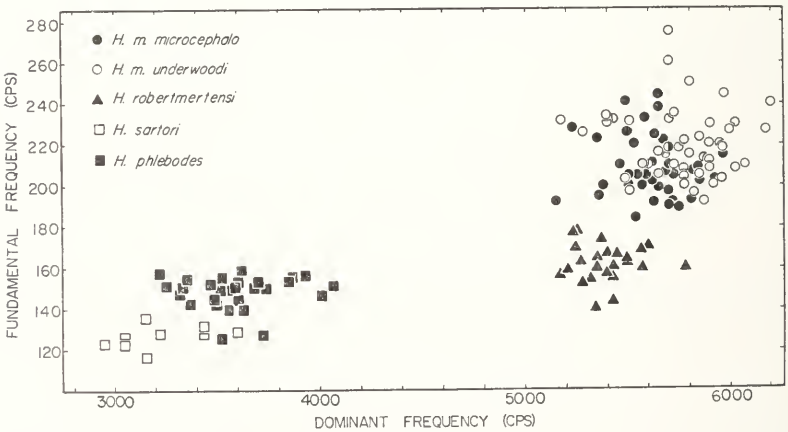


FIG. 9. Scatter diagram relating the dominant and fundamental frequencies of the normal primary notes in the *Hyla microcephala* group. Each symbol represents a different individual.

Repetition rate.—The repetition rate of the secondary notes, in calls consisting of more than one secondary, was measured for each form. A considerable amount of variation in this parameter was found in all of the taxa (Table 5). This variation probably is due in part to the effect of temperature differences. Repetition rate is

the only parameter analyzed for which there is a correlation with the air-temperature, but even here the correlation is weak, probably due to the microenvironmental effects of humidity, air-movement, and other factors in addition to the ambient air temperature that influences the body temperature of the frogs. These rates are nearly alike in both subspecies of *H. microcephala* and in *phlebodes*. The repetition rates in *H. robertmertensi* and *H. sartori* are considerably faster than in the other three taxa. *Hyla sartori* has the fastest repetition rate of the group.

In all characteristics of the mating calls the two subspecies of *H. microcephala* agree closely, as might be expected, although the differences are statistically significant. *Hyla robertmertensi* is distinctive in call pattern and seems to be closer to *microcephala* in dominant frequency but closer to *H. phlebodes* in fundamental frequency. Thus, it is somewhat intermediate between *microcephala* and *phlebodes*. The identical pattern and similarity in fundamental and dominant frequencies of the calls of *H. phlebodes* and *H. sartori* possibly indicate close relationship.

Geographic variation in call.—Hyla m. microcephala has higher fundamental and dominant frequencies in Costa Rica than in Panamá. In Costa Rican *H. m. underwoodi* the fundamental and dominant frequencies are lower than in other parts of the range. Frogs of this subspecies recorded in Nicaragua and Honduras have slightly lower dominant frequencies and higher fundamental frequencies than those recorded in Guatemala or Oaxaca. The duration of both primary and secondary notes decreases to the south; samples from Nicaragua and Costa Rica have the shortest notes. Comparison of duration of notes in the two subspecies shows that the Panamanian *H. m. microcephala* have slightly longer notes than do any *H. m. underwoodi;* the more northern populations of *H. m. underwoodi* from México most closely approach *H. m. microcephala* in this characteristic.

The calls of *H. robertmertensi* in Oaxaca have higher dominant and fundamental frequencies and longer secondary notes than do those in Chiapas.

The calls of *H. phlebodes* recorded at Puerto Viejo, Costa Rica, have slightly lower dominant frequencies than do those recorded at Turrialba, Costa Rica, and in Panamá, whereas those recorded at Turrialba have lower fundamental frequencies than in other samples. The duration of notes is slightly shorter in both Costa Rican samples than in those recorded in Panamá.

LIFE HISTORY

The frogs of the *Hyla microcephala* group breed in shallow grassy ponds. In some places they breed in permanent ponds, but usually congregate around temporary pools, such as depressions in forests, flooded fields, and roadside ditches. At the height of their breeding season, usually in the early part of the rainy season, the congregations are made up of large numbers of individuals. In April, 1961, and in June, 1966, the senior author noted nearly continuous choruses of *H. m. microcephala* in roadside ditches along the 75 kilometers of road between Villa Neily and Palmar Sur, Puntarenas Province, Cost Rica; on June 20, 1966, at Puerto Viejo, Heredia Province, Costa Rica, he estimated approximately 900 *Hyla phlebodes* in one pond, and two nights later noticed that the number of individuals ad increased substantially. Other observations by the first author on size of breeding congregations include nearly continuous choruses of *H. m. underwoodi* between Villahermosa and Teapa, Tabasco, in July of 1958, an estimated 400 *Hyla robertmertensi* in a road side ditch 7.2 kilometers west-northwest of Zanatepec, Oaxaca, on July 13, 1956, and approximately 150 *Hyla sartori* around a rocky pool in a riverbed, 11.8 kilometers west-northwest of Tierra Colorada, Guerrero, on June 28, 1958.

The length of the breeding season seemingly is more dependent on climatic conditions in various parts of Middle America than on behavioral differences in the various species. Thus, Fouquette (1960b) found in the Canal Zone that *H. m. microcephala* formed breeding choruses from May through January, the entire rainy season in that area. In the wetter coastal region of Puntarenas Province, Costa Rica, the species breeds as early as mid-March, whereas in the drier region encompassing Guanacaste Province, Costa Rica, and southwestern Nicaragua breeding activity is initiated by the first heavy rains of the season, usually in June.

Hyla phlebodes inhabits regions having rainfall throughout the year. Although large breeding congregations are most common in the early parts of the rainy season, males probably call throughout the year. At Puerto Viejo in Costa Rica the senior author has heard *Hyla phlebodes* in February, April, June, July, and August. Charles W. Myers noted calling males of this species in the area around Almirante, Bocas del Toro Province, Panamá, in September, October, and February. An exception to the correlation between rainfall and breeding activity was noted by the junior author in *Hyla phlebodes* in the Canal Zone, where he noticed a decrease in activity of that species in October and November, when the rains are heaviest and

most frequent. Furthermore, independent observations made by both of us indicate that *H. phlebodes* does not reach peaks of activity during or immediately after heavy rains, but instead builds up to peaks of activity two or three days after a heavy rain. This is in contrast to the other species, all of which characteristically inhabit drier environments than does *H. phlebodes*. Peaks of breeding activity in the other species occur immediately after, or even during, heavy rains.

The calling location of the males generally is on vegetation above, or at the edge of, the water. *Hyla microcephala* and *H. phlebodes* call almost exclusively from grasses and sedges; *phlebodes* usually calls from taller and more dense grasses than does *microcephala*. Except for some minor differences in calling location observed by the junior author (Fouquette, 1960b) in the Canal Zone, the differences in density and height of grasses utilized for calling-locations probably is dependent primarily on the nature of the available vegetation. Although bushes and broad-leafed herbs are usually present at the breeding sites, males of these species seldom utilize them for calling locations. Both *H. robertmertensi* and *H. sartori* have been observed calling from grasses, herbs, bushes, and low trees. Calling males of *robertmertensi* have been found two meters above the ground in small trees.

Daytime retreats in the breeding season sometimes are no more than shaded clumbs of vegetation adjacent to a pond or in clumps of grass in a pond. Individuals of *H. m. underwoodi* were found by day under the outer sheaths of banana plants next to a water-filled ditch. Dry season refuges are unknown.

Amplexus is axillary in all four species. Egg deposition has been observed in *H. m. microcephala, m. underwoodi,* and *phlebodes*. In all three the eggs are deposited in small masses that float near the surface of the water and usually are at least partly attached to emergent vegetation. Each clutch does not represent the entire egg complement of the female.

Tadpoles are definitely known of only *H. m. microcephala* and *phlebodes;* these have been described in the preceding accounts of the species. The tadpoles of these two species can be distinguished readily (Pl. 15). The tadpole of *H. microcephala* has a uniformly white venter and nearly transparent tail, whereas in *H. phlebodes* the venter is flecked anteriorly and the tail is mottled. In life, *H. microcephala* is easily recognized by the orange posterior half of the tail, whereas the tail in *H. phlebodes* is mottled tan and grayish brown.

PHYLOGENETIC RELATIONSHIPS

The evidence already presented on osteology, external structure, coloration, mating call, and life history emphatically show that the four species under consideration are a closely related assemblage. Now the question arises: To what other groups in the genus is the *Hyla microcephala* group related? Furthermore, it is pertinent to this discussion to attempt a reconstruction of the phylogeny of the group as a whole and of the individual species in the *Hyla microcephala* group. With regard to the relationships of the group we must take into account certain species in South America. Our endeavors there are hampered by the absence of data on the mating calls and life histories of most of the relevant species.

As mentioned in the acount of *Hyla m. microcephala,* the species *microcephala* possibly is subspecifically related to *Hyla misera,* a frog widespread in the Amazon Basin. *Hyla misera* resembles *microcephala* in coloration, external structure, and cranial characters. The frontoparietals are equally poorly ossified, and the frontoparietal fontanelle is extensive. Our principal reason for not considering the two taxa conspecific at this time is our lack of knowledge concerning the color of living *H. misera,* the structure of the tadpoles, and the characteristics of the mating call. Even with the absence of such data that we think essential to establish the nomenclature status of the taxa, we are confident that the two are sufficiently closely related that any discussion of the phylogenetic relationships of one species certainly must involve consideration of the other.

Hyla misera possibly is allied to other small yellowish tan South American *Hyla* that lack dark pigmentation on the thighs. Probable relatives are *Hyla elongata, minuta* (with *goughi, pallens, suturata, velata,* and possibly others as synonyms), *nana,* and *werneri.* The consideration of the interspecific relationships of these taxa is beyond the scope of this paper, but we can say that each of these species has a pale yellowish tan dorsum, relatively broad dorsolateral brown stripe, and narrow longitudinal brown lines or irregular marks on the dorsum. Furthermore, examination of the skulls of *elongata, nana,* and *werneri* reveals that they are like *misera* and *microcephala* in the nature of the frontoparietal fontanelle and in having a greatly reduced quadratojugal. Thus, on the basis of cranial and external characters the *Hyla microcephala* group can be associated with *Hyla misera* and its apparent allies in South America. This association can be only tentative until the mating calls, tadpoles, and chromosome numbers of the South American species are known.

Among the Middle American hylids, only the *Hyla microcephala* group and *H. ebraccata* have a haploid number of 15 chromosomes (Duellman and Cole, 1965). All other New World *Hyla,* for which the number is known, have a haploid number of 12; the only other *Hyla* having 15 is a Papuan *Hyla angiana* (Duellman, 1967).

Hyla ebraccata occurs in the humid tropical lowlands of Middle America and the Pacific lowlands of northwestern South America. It is the northernmost, and only Central American, representative of the *Hyla leucophyllata* group, which is diverse (about 10 species currently recognized) and widespread in tropical South America east of the Andes. This group is characterized by having broad, flat skulls with larger nasals and more ossification of the frontoparietals than in the *Hyla microcephala* group. The quadratojugal is present as a small anteriorly projecting spur that does not connect with the maxillary. Externally, the *Hyla leucophyllata* group is characterized by having a well-developed axillary membrane, uniformly yellow thighs, and a dorsal color pattern in many species consisting of a dark lateral band, a pale dorsolateral band or dorsal ground color, and a large middorsal dark mark. In some species, the dorsal pattern consists of small dark markings or is nearly uniformly pale. At least in the Central American *Hyla ebraccata,* the mating call consists of a single primary note followed by a series of shorter secondary notes, the tadpoles have xiphicercal tails and lack teeth, and the haploid number of chromosomes is 15. On the strength of these observations it seems imperative to consider the *Hyla leucophyllata* group as a close ally to the *Hyla microcephala* group. Successful artificial hybridization supports the close relationship of *H. m. microcephala* and *phlebodes;* partial success of artificial hybridization of these two with *ebraccata* (Fouquette, 1960b) provides further evidence for close relationship between the *Hyla leucophyllata* and *Hyla microcephala* groups.

In México and northern Central America two small species, *Hyla picta* and *Hyla smithi,* comprise the *Hyla picta* group. These frogs resemble members of the *Hyla microcephala* group by having a yellowish tan dorsum with a dorsolateral white stripe and uniformly yellow thighs. Furthermore the mating call is not unlike those of the species in the *Hyla microcephala* group. Despite these similarities, the *Hyla picta* group differs from the *Hyla microcephala* group by having a well-developed quadratojugal that connects to the maxillary, tadpoles with teeth present and caudal fins completely enclosing the caudal musculature, and a haploid number of 12 chromosomes. In all of these characteristics the frogs of the

Hyla picta group more closely resemble other Middle American *Hyla* than they do the *Hyla microcephala* group. Therefore, it can best be presumed that the superficial resemblances of coloration and the mating call are the result of convergence.

Since the *Hyla microcephala* and *leucophyllata* groups apparently are related and since the greatest diversity of these frogs is in South America (if *Hyla misera* and its relatives are placed with the *Hyla microcephala* group), it seems appropriate to place the centers of origins of these groups in South America. Therefore, the *Hyla microcephala* group and *Hyla ebraccata* of the *Hyla leucophyllata* group either have immigrated into Central America, or they are representatives of those groups that were isolated in Central America during most of the Cenozoic when South America was separated from Central America.

The interspecific relationships of the species in the *Hyla microcephala* group are not clear. On the basis of coloration, *H. m. microcephala* and *H. robertmertensi* are close, and *H. m. underwoodi* and *H. phlebodes* are nearly identical. The mating calls of *H. phlebodes* and *sartori* closely resemble one another, whereas the call of *robertmertensi* is intermediate between these and *microcephala.*

In most respects *Hyla microcephala* is distinct from the other species, and with the exception of the amount of ossification of the frontoparietals, the other species can be easily derived from a *microcephala*-like ancestor. Possibly the slightly increased ossification of the frontoparietals in *robertmertensi, phlebodes,* and *sartori* is secondary, or possibly after differentiation of the species the amount of ossification was further reduced in *microcephala.* If so, the species fall into a reasonable phylogenetic scheme that has *microcephala* as the extant species most like the ancestral stock.

We visualize the evolutionary history of the group to have followed a course that began with the invasion of Central America by a *microcephala* ancestral stock that differentiated into two populations in lower Central America—a *microcephala*-like frog on the Pacific lowlands and a *phlebodes*-like frog on the Caribbean lowlands. Differentiation could have been brought about by isolation by montaine or marine barriers. The population on the Pacific lowlands either was preadapted for subhumid conditions or became so adapted and dispersed northward onto the Pacific lowlands of northern Central America. Simultaneously the frogs on the Caribbean lowlands, which were adapted to humid environments, dispersed northward in the humid forested regions to southern México and crossed the Isthmus of Tehuantepec onto the Pacific slopes of

Oaxaca and Guerrero northward to Jalisco. Subsequent development of arid conditions, possibly in the Pliocene, Pleistocene, or even as late as the Thermal Maximum in post-Wisconsin time, resulted in a restriction of the ranges in northern Central America, thereby isolating part of the *phlebodes*-stock on the Pacific slopes of México, where it adapted to drier conditions and evolved into *sartori*. The rest of the *phlebodes*-stock was restricted to the humid forests on the Caribbean lowlands of lower Central America. The increased aridity on the Pacific lowlands eliminated the *microcephala*-stock from southern Honduras and northwestern Nicaragua and in so doing left an isolated population on the lowlands of Chiapas and Guatemala, which differentiated into *robertmertensi*. The original stock on the Pacific lowlands of Panamá and southeastern Costa Rica became *microcephala*.

If the *microcephala*-stock was, as we believe, better adapted for existence under subhumid conditions than was the *phlebodes*-stock, the development of subhumid conditions in much of the lowland region of northern Central America and southern México would have permitted the expansion of the range of *microcephala* into the area now inhabited by *H. m. underwoodi*, while *phlebodes* was being eliminated from this area by climatic conditions that were unsuited to its survival there. Perhaps the similarity in coloration of *H. m. underwoodi* and *phlebodes* is the result of convergence or possibly hybridization occurred at the time the former was expanding its range and the latter's range was being restricted. If hybridization did occur, the differences in mating call subsequently were enhanced, thereby providing a valid isolating mechanism in sympatric populations.

Hyla microcephala and *phlebodes* range into northern South America. Probably both species entered South America in relatively recent times after they had differentiated from one another in Central America.

LITERATURE CITED

Boulenger, G. A.

1898. Fourth report on additions to the batrachian collection in the Natural-History Museum. Proc. Zool. Soc. London, 1898, pp. 873-482, pls. 38-39. October 1.

1899. Descriptions of new batrachians in the collection of the British Museum (Natural History). Ann. Mag. Nat. Hist., ser. 7, 3:273-277, pls. 11-12.

Breder, C. M. Jr.

1946. Amphibians and reptiles of the Rio Chucunaque Drainage, Darien, Panama, with notes on their life histories and habits. Bull. Amer. Mus. Nat. Hist., 86:375-436, pls. 42-60, August 26.

Cole, L. J. and Barbour, T.

1906. Vertebrata from Yucatan: Reptilia; Amphibia; Pisces. Bull. Mus. Comp. Zool., 50:146-159. November.

Cope, E. D.

1886. Thirteenth contribution to the herpetology of tropical America. Proc. Amer. Philos. Soc., 23:271-287. February 11.

1894. Third addition to a knowledge of the Batrachia and Reptilia of Costa Rica. Proc. Acad. Nat. Sci. Philadelphia, 1894, pp. 194-206.

Duellman, W. E.

1956. The frogs of the hylid genus *Phrynohyas* Fitzinger, 1843. Misc. Publ. Mus. Zool., Univ. Michigan, 96:1-47, pls. 1-6 February 21.

1967. Additional studies of chromosomes of anuran amphibians. Syst. Zool., 16:38-43, March 17.

Duellman, W. E. and Cole, C. J.

1965. Studies of chromosomes of some anuran amphibians (Hylidae and Centrolenidae). Syst. Zool., 14:139-143. July 9.

Duellman, W. E. and Trueb, L.

1966. Neotropical hylid frogs, genus Smilisca. Univ. Kansas Publ., Mus. Nat. Hist., 17:281-375, pls. 1-12. July 14.

Dunn, E. R.

1931. The amphibians of Barro Colorado Island. Occas. Papers Boston Soc. Nat. Hist., 5:403-421. October 10.

1933. Amphibians and reptiles from El Valle de Anton, Panamá. *Ibid.*, 8:65-79. June 7.

1934. Two new frogs from Darien. Amer. Mus. Novit., 747:1-2. September 17.

Fouquette, M. J. Jr.

1960a. Call structure in frogs of the family Leptodactylidae. Texas Jour. Sci., 12:201-215. October.

1960b. Isolating mechanisms in three sympatric tree frogs in the Canal Zone. Evolution, 14:484-497. December 16.

Gaige, H. T., Hartweg, N. and Stuart, L. C.

1937. Notes on a collection of amphibians and reptiles from eastern Nicaragua. Occas. Papers Mus. Zool., Univ. Michigan, 357:1-18. October 26.

Gosner, K. L.

1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica, 16:183-190. September 23.

KELLOGG, R.
1932. Mexican tailless amphibians in the United States National Museum. Bull. U. S. Natl. Mus., 160:1-224. March 31.

RIVERO, J. A.
1961. Salientia of Venezuela. Bull. Mus. Comp. Zool., 126:1-207. November.

SMITH, H. M.
1951. The identity of *Hyla underwoodi* Auctorum of Mexico. Herpetologica, 7:184-190. December 31.

STEJNEGER, L.
1906. A new tree toad from Costa Rica. Proc. U. S. Natl. Mus., 30:817-818. June 4.

STUART, L. C.
1935. A contribution to a knowledge of the herpetology of a portion of the savanna region of central Petén, Guatemala. Misc. Publ. Mus. Zool., Univ. Minchigan, 29:1-56, pls. 1-4. October 4.

TAYLOR, E. H.
1952. The frogs and toads of Costa Rica. Univ. Kansas Sci. Bull., 35-577-942. July 1.

Transmitted July 11, 1967.

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Descriptions of New Hylid Frogs From México and Central America

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Biological exploration of México and Central America has revealed the presence of a diverse fauna, elements of which have undergone speciation in separate areas within the relatively small region. Some genera of amphibians, especially *Eleutherodactylus* and *Hyla*, are represented by many species having small geographic ranges in México and Central America. Most of the species of *Hyla* inhabiting the lowlands have been known to science for many years, and most of the novelties today are found in the less accessible highlands. No fewer than 19 new species of hylid frogs have been discovered and named from México and Central America in the past decade.

In the spring and summer of 1966 I studied hylid frogs in many parts of southern México and Central America; the field work was designed to obtain specimens and data that would resolve certain systematic problems. To a certain extent the studies were successful, but in the course of the work five previously unknown hylids were discovered; these are named and described in this paper. The only species described herein that I do not know in life is one of *Plectrohyla* that has been represented in museum collections for several years but was not obtained in my own field work.

In this paper I am presenting diagnoses, descriptions, and brief comments on the relationships of five new species and one subspecies. More exhaustive accounts will be included in a monograph, now in preparation, on the Middle American hylids.

For use of comparative material used in the preparation of this paper, I am indebted to Richard J. Baldauf, Texas Cooperative Wildlife Collection (TCWC); Charles M. Bogert, American Museum of Natural History (AMNH); James A. Peters, United States National Museum (USNM); Hobart M. Smith, University of Illinois Museum of Natural History (UIMNH); Charles F. Walker, University of Michigan Museum of Zoology (UMMZ); and Ernest E. Williams, Museum of Comparative Zoology (MCZ). KU refers to the University of Kansas Museum of Natural History. I am

especially grateful for help in obtaining specimens and data to Linda Trueb, who accompanied me throughout México and Central America, where we were joined by John D. Lynch in Costa Rica and Charles W. Myers in Panamá. Linda Trueb offered helpful suggestions in the course of preparing the manuscript, and David M. Dennis skillfully prepared the illustrations which more accurately depict the frogs than my written descriptions; both of these persons have my thanks for their contributions.

Ratibor Hartmann of Finca Santa Clara, Chiriquí, Panamá, made possible our travels to the Río Changena on the Atlantic slopes of Bocas del Toro. Field work in Costa Rica was facilitated by the Organization of Tropical Studies through the courtesy of Stephen B. Preston and Norman Scott. Rodolfo Hernandez Corzo of the Dirección General de la Fauna Silvestre provided the necessary permits to collect in México. I thank each of these persons for his helpfulness and cooperation.

Field work in México and Central America and the associated laboratory studies on Middle American hylid frogs are supported by grants from the National Science Foundation (GB-1441 and GB-5818). The field work in Panamá was part of a survey of the herpetofauna of that country carried out in cooperation with the Gorgas Memorial Laboratory and supported by the National Institutes of Health (GM-12020).

Hyla xanthosticta new species

Plate 17

Holotype.—Adult female, KU 103772, from the south fork of the Río Las Vueltas on the south slope of Volcán Barba, near the northwest base of Cerro Chompipe, Heredia Province, Costa Rica, elevation 2100 meters; obtained on June 26, 1966, by John D. Lynch.

Diagnosis.—A member of the *Hyla pictipes* group (Starrett, 1966), characterized by having dorsum uniform green, canthal stripe bronze-color, flanks and anterior and posterior surfaces of thighs dark brown with bright yellow spots, throat and belly yellow, and hands having only vestigial web.

Description of holotype.—Female having a snout-vent length of 29.3 mm.; tibia length 16.2 mm., 55.3 per cent of snout-vent length; foot length (measured from proximal edge of inner metatarsal tubercle to tip of longest toe) 14.1 mm., 48.1 per cent of snout-vent length; head length 10.0 mm., 34.1 per cent of snout-vent length; head width 10.3 mm., 35.2 per cent of snout-vent length. Snout in lateral profile truncate, slightly inclined posteroventrally, in dorsal profile narrow but truncate; canthus angular; loreal region barely concave; lips thick, barely flared. Snout long; distance from anterior corner of eye to nostril equal to diameter of eye; nostrils slightly protuberant, directed laterally; internarial distance, 2.6 mm.; internarial area slightly depressed; top of head

slightly convex; interorbital distance 3.2 mm., 31.1 per cent of width of head; width at eyelid 2.6 mm.; 24.3 per cent of width of head. Diameter of eye 3.0 mm.; thin dermal fold extending posteriorly from posterior corner of eye, above tympanum, to point above insertion of arm. Tympanum distinct, its diameter half that of eye.

Axillary membrane absent; arms slender; thin scalloped dermal fold on ventrolateral edge of forearm; thin dermal fold on wrist; fingers long, tapering; length of fingers from shortest to longest, 1-2-4-3; discs small, only slightly wider than digits; subarticular tubercles large; distal tubercle on third finger broad, flat; distal tubercle on fourth finger strongly bifid; supernumerary tubercles large, round, closely spaced irregularly on proximal segments of digits; prepollex moderately enlarged. Web lacking between first and second fingers, vestigial between second and third fingers, extending from middle of antepenultimate phalanx of third to base of penultimate phalanx of fourth. Heels overlap by about one-third length of shank when hind limbs adpressed; tibiotarsal articulation extends to anterior edge of eye; thin transverse dermal fold on heel; scalloped dermal fold along outer edge of tarsus; inner metatarsal tubercle large, flat, elliptical, visible from above; toes long, slender; length of toes from longest to shortest, 1-2-5-3-4; discs small, barely wider than digits; subarticular tubercles large, round, subconical; supernumerary tubercles few, scattered on proximal segments of digits; toes about two-thirds webbed; webbing extending from middle of penultimate phalanx of first toe to middle of penultimate phalanx of second, from distal end of penultimate phalanx of second to base of penultimate of third, from distal end of penultimate phalanx of third to middle of antepenultimate of fourth to middle of penultimate of fifth toe.

Anal opening directed posteroventrally at level of mid-thigh, bordered below by large tubercles; anal sheath lacking. Skin smooth on dorsum except for small scattered tubercles, granular on belly and posteroventral surfaces of thighs. Tongue round, emarginate, barely free behind. Prevomerine teeth 5-5, on large ovoid elevations at level of posterior edges of small round choanae.

Color (in preservative): dark purplish brown above, brown on limbs; first three fingers and first three toes creamy yellow; other digits brown; flanks dark brown with white spots; anterior and posterior surfaces of thighs and inner surfaces of shanks brown with cream-colored spots. White stripes on edge of upper lip, ventrolateral edge of forearm, outer edge of tarsus, and above anus. Chin and throat white; belly and ventral surfaces of limbs cream-color.

Color (in life): dorsum green, palest on sides of head; dorsal surfaces of thighs tan; canthal stripe bronze-tan (reddish copper at night); flanks, anterior and posterior surfaces of thighs, and inner surfaces of tarsi brown with bright yellow spots. Throat and belly pale yellow; ventral surfaces of limbs dull, dark yellow; large, bright yellow spot on anteroventral surface of thigh; bright yellow tubercles on median part of ventral surface of thigh. Anal area dark brown with white stripe above and yellow stripe below; white stripe on outer edge of forearm, outer edge of tarsus, and edge of upper lip. Iris gold-color with fine black reticulations and faint reddish suffusion medially; palpebral membrane clear.

Comparisons.—*Hyla xanthosticta* is a member of the *Hyla pictipes* group that contains *debilis, pictipes, rivularis,* and *tica.* From all of these, *xanthosticta* differs by having large yellow spots on the flanks and thighs, a white

labial stripe, and a large yellow spot on the proximal ventral surface of each thigh. Females of *Hyla pictipes* have small creamy yellow spots on the flanks and thighs but have dark spots on the venter; furthermore, *pictipes* lacks white stripes on the upper lip and above the anus, lacks a canthal stripe, and has larger discs and less webbing on the hand. *Hyla tica* differs from *xanthosticta* by having white mottling on the flanks, dark transverse bands on the limbs, and larger discs, and lacks yellow spots on the thighs, and white stripes on the upper lip, limbs, and above the anus. *Hyla rivularis* is notably different in having a tan dorsum and creamy yellow venter with black flecks; moreover, *rivularis* lacks spots on the flanks and thighs and white stripes on the upper lip, limbs, and above the anus. Of all of the species in the *pictipes* group, *xanthosticta* most closely resembles *debilis*. This species has a dull green dorsum, usually flecked with brown or black, and a creamy white venter. The flanks of *debilis* are creamy white with small brown flecks, and the anterior and posterior surfaces of the thighs are bright yellow. *Hyla debilis* has a dull tan canthal stripe and white spots on the upper lip; the webbing on the hand is slightly more extensive, and the discs are slightly larger, in *debilis* than in *xanthosticta*.

The presence of the large yellow spots on the flanks and thighs in combination with the uniformly green dorsum and yellow venter immediately distinguishes *Hyla xanthosticta* from all other known species of Middle American hylids.

Remarks.—The only known specimen of *Hyla xanthosticta* was perched at night on a leaf about one meter above the ground. The frog was found in humid upper montane forest characterized by large oaks supporting many bromeliads and heavy growths of mosses. Two other members of the *Hyla pictipes* group—*pictipes* and *rivularis*—were abundant along a stream in the oak forest.

The specific name is derived from the Greek *xanthos* meaning yellow and the Greek *stiktos* meaning spotted, and alludes to the diagnostic yellow spots on the flanks and thighs.

Hyla pseudopuma infucata new subspecies

Plate 17

Holotype.—Adult male, KU 101770 from the Río Changena, Bocas del Toro Province, Panamá, elevation 830 meters; obtained May 18, 1966, by William E. Duellman.

Paratypes.—KU 101771-80; MCZ 55251-2, and UMMZ 126811-12, same locality; collected May 18-22, 1966, by William E. Duellman.

Diagnosis.—A subspecies of *Hyla pseudopuma* characterized by having dark red, instead of yellow, in groin and on anterior and posterior surfaces of thighs; white stripe above anal opening; and blunt snout.

Description of holotype.—Adult male having a snout-vent length of 37.8 mm.; tibia length 20.6 mm., 54.4 per cent of snout-vent length; foot length (measured from proximal edge of inner metatarsal tubercle) 18.6 mm., 49.2 per cent of snout-vent length; head length 11.9 mm., 31.4 per cent of snout-vent length; head width 11.4 mm., 30.1 per cent of snout-vent length. Snout in lateral profile bluntly rounded, in dorsal profile truncate; canthus rounded;

loreal region barely concave; lips thick, moderately flared. Snout short, distance from anterior corner of eye to nostril equal to about three-fourths diameter of eye; nostrils slightly protuberant, directed dorsolaterally; internarial distance 2.6 mm.; internarial area not depressed; top of head flat; interorbital distance 3.8 mm., 33.3 per cent of width of head; width of eyelid 3.2 mm., 28.2 per cent of width of head. Eye large, protuberant, diameter 4.3 mm.; thin dermal fold extending posteriorly from posterior corner of eye, obscuring upper edge of tympanum, curving downward to point above insertion of arm. Tympanum distinct except dorsally, its diameter 51.1 per cent that of eye, separated from eye by distance equal to diameter of tympanum.

Axillary membrane absent; arms moderately robust; dermal fold on outer edge of forearm indistinct, interrupted; transverse fold on wrist weak; fingers short, stocky; length of fingers from shortest to longest, 1-2-4-3; discs large, width of that on third finger 2.6 mm., larger than tympanum; subarticular tubercles moderately small, flat, none distinctly bifid; supernumerary tubercles conical, present on proximal segments; prepollex enlarged, bearing nuptial excrescence composed of many minute horny spinules; webbing absent between first and second fingers, extending from middle of antepenultimate phalanx of second to base of antepenultimate phalanx of third and beyond to base of penultimate phalanx of fourth finger. Heels overlap by about one-third length of tarsus when hind limbs adpressed; tibiotarsal articulation extends to anterior corner of eye; transverse dermal fold on heel; tarsal fold absent; inner metatarsal tubercle long, elliptical, flat, barely visible from above; outer metatarsal tubercle small, conical; toes moderately long, stout; length of toes from shortest to longest, 1-2-3-5-4; discs nearly as large as those on fingers; subarticular tubercles small, flat; supernumerary tubercles large, conical, pigmented, in single row on proximal segments of each toe; toes about two-thirds webbed; webbing extending from distal end of penultimate phalanx of first toe to base of penultimate phalanx of second, from distal end of penultimate phalanx of second to middle of antepenultimate of third, from distal end of penultimate phalanx of third to base of penultimate of fourth to distal end of penultimate of fifth toe.

Anal opening directed posteriorly at level of upper surfaces of thighs, bordered below by vertical flesh folds; anal sheath absent. Skin of belly, ventral surfaces of arms, and proximal posteroventral surfaces of thighs granular, elsewhere smooth. Tongue ovoid, about twice as long as wide, shallowly notched posteriorly, barely free behind. Prevomerine teeth 5-6, situated on transverse ridges between posterior borders of small round choanae. Vocal slit extending from midlateral edge of tongue to angle of jaw.

Color (in preservative): dorsum grayish tan with large brown blotch extending from eyelids to middle of back, limbs marked with brown transverse bars, 2 on each forearm, 3 on each thigh, shank, and foot. Flanks dark gray with white spots; groin, anterior and posterior surfaces of thighs, ventral surfaces of shanks, and inner edges of feet orange-tan; anal region dark brown, bordered above by white stripe; belly and chin creamy white, latter with grayish brown flecks.

Color (in life): dorsum yellowish tan with olive-brown markings by night and uniform pale yellowish tan by day; axilla, inner surface of elbow, groin, anterior and posterior surfaces of thighs, ventral surfaces of thighs and shanks, inner surfaces of feet, and dorsal surfaces of first three toes tomato red; flanks

dark blue with yellow spots and reticulations. Throat, chest, and anterior part of belly creamy white; posterior part of belly orange, becoming red in extreme posterior region; throat flecked with brown; iris pale bronze with black reticulations; palpebral membrane clear above, yellowish tan below; nuptial excrescenses dark brown.

Variation.—The discussion of variation is based on the type series plus 31 specimens (KU 101781-811) from the Río Claro near its junction with the Río Changena, at an elevation of 910 meters. Females are slightly larger than males, but do not differ significantly in proportions (Table 1). All specimens have the diagnostic red legs and blue flanks with yellow spots or mottling, but the dorsal pattern is highly variable. In most individuals the dark markings on the dorsum are a solid color, but in some the borders of the marks are dark, and the interior of each mark is nearly the same color as the rest of the dorsum. A triangular dark mark with the anterolateral corners on the eyelids is present in all specimens. In some individuals the posteriorly directed apex of this triangular mark is connected to the apex of another triangular mark on the back; in other individuals the marks are narrowly separated, whereas in a few specimens the marks are broadly connected. A dark blotch usually is present on the posterior end of the body. One specimen (KU 101771) has many small white spots on the dorsum. The white stripe above the anus is invariably present, and the transverse bars on the limbs are present in all specimens, although they are indistinct in some individuals. The pattern on the flanks varies from three or four large spots to many (30-44) small spots. All males have dark flecks or reticulations on the throat; in some individuals the chest and belly are heavily flecked. Although the amount of flecking is much less in most females, one individual is as heavily flecked on the throat and belly as any male.

The change in coloration in this frog is noteworthy. The following description of metachrosis in seven specimens from the Río Claro illustrates the change. At night the frogs were yellowish tan above with slightly darker dorsal markings. The axilla, groin, anterior and posterior surfaces of the thighs, ventral surfaces of the hind limbs, and webbing on the hands and feet were tomato red. By day, some individuals became creamy yellow, others ashy white, and others grayish tan. The flanks were dark blue with yellow spots.

Comparisons.—The population of frogs described here closely resembles *Hyla pseudopuma* Günther in the highlands of Costa Rica. Both have the same kind of, and variation in, dorsal markings; conical, pigmented supernumerary tubercles on the toes; bilobate vocal sac; and large prepollex bearing horny nuptial spinules. Although at present no evidence for intergradation exists, the population described here is considered to be a subspecies of *Hyla pseudopuma.*

The two subspecies exhibit few differences in size and proportions, except that the tympanum is larger in *pseudopuma* (Table 1). *Hyla p. pseudopuma* has dark brown or yellowish tan thighs and brown flanks with a few creamy white spots; the groin in some specimens is pale blue. The red color on the limbs characteristic of *infucata* is lacking in *pseudopuma*, which also lacks the white stripe above the anus characteristic of *infucata.* The only noticeable morphological difference between the subspecies, except in the size of the tympanum, is the shape of the snout. In *infucata* the snout is bluntly rounded in lateral profile and truncate in dorsal profile, whereas in *pseudopuma* the

Table 1.—Variation in Certain Measurements and Proportions in the Subspecies of Hyla pseudopuma. (Means Are Given in Parentheses Below the Observed Range.)

Subspecies	Sex	N	Snout-vent length	Tibia length/ S-V L	Foot length/ S-V L	Tympanum/ eye
H. p. pseudopuma	♂	31	37.6–41.4 (39.7)	48.5–55.0 (51.5)	44.7–52.9 (48.2)	47.6–66.7 (57.6)
H. p. infucata	♂	31	37.6–42.9 (39.5)	50.7–56.9 (53.4)	43.3–49.5 (47.4)	41.8–55.3 (49.2)
H. p. pseudopuma	♀	11	41.6–47.6 (44.3)	49.1–53.8 (51.7)	45.4–49.5 (47.6)	57.9–71.4 (60.2)
H. p. infucata	♀	11	41.1–45.6 (42.6)	50.0–55.4 (52.6)	43.5–47.4 (45.8)	47.6–56.1 (50.1)

snout is more acutely rounded in lateral profile and acuminate in dorsal profile (Fig. 1). This external difference is correlated with the nature of the underlying premaxillaries. In *infucata* the premaxillaries lie in a transverse plane and have short, nearly vertical alary processes, whereas in *pseudopuma* the premaxillaries lie at a slight angle and have longer alary processes that are inclined posteriorly.

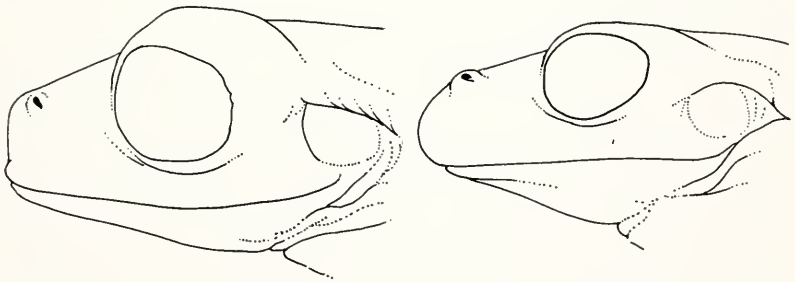


Fig. 1. Lateral views of the heads of *Hyla pseudopuma pseudopuma* (left, KU 64884) and *H. p. infucata* (right, KU 101784). × 4.

The only other frog in Central America having red webs and anterior and posterior surfaces of the thighs is *Hyla loquax*, which has a broad head, extensive axillary membrane, single median vocal sac, and uniformly creamy yellow flanks; furthermore, *loquax* lacks conical, pigmented supernumerary tubercles on the toes and a large prepollex with horny nuptial spinules. *Hyla rufitela* has red webbing, but in no other diagnostic feature resembles *infucata*, for *rufitela* is green above, white below, and has angular prevomerine dentigerous ridges.

Remarks.—Most specimens of *Hyla pseudopuma infucata* were found on

bushes and low trees at night. Three males and one clasping pair were on the ground. The habitat is humid lower montane forest where the amount of rainfall is high. Although no breeding was observed nor calls heard, it is presumed that this subspecies breeds in shallow, temporary pools, like those utilized by the nominate subspecies.

The two localities where *Hyla pseudopuma infucata* is known are in the maze of ridges north of Cerro Pando on the Panamanian-Costa Rican border. The Río Claro is a tributary of the Río Changena, in turn a tributary of the Río Changuinola, which receives many streams and rivers draining the northern slopes of the highlands in Bocas del Toro Province before flowing into the Caribbean. We reached the Río Claro and Río Changena by walking from Finca Santa Clara on the Pacific slopes, over the continental divide, and down the north slope of Cerro Pando.

The subspecific name is derived from the Latin *infucatus*, meaning painted, in allusion to the red colors on the limbs and webs.

Hyla pellita new species

Plate 18

Holotype.—Adult male, KU 100970 from 33 kilometers north of San Gabriel Mixtepec, Oaxaca, México, elevation 1675 meters; obtained on February 20, 1966, by William E. Duellman and Linda Trueb.

Paratypes.—KU 100971-2 collected with the holotype and KU 100974-5 from 30 kilometers north of San Gabriel Mixtepec, Oaxaca, México, elevation 1530 meters; same date and collectors.

Diagnosis.—A small yellowish tan *Hyla* characterized by tympanum concealed, anal opening not bordered below by large tubercles, brown bands on shanks, and dark flecks on roof of mouth anteriorly.

Description of holotype.—Adult male having snout-vent length of 27.3 mm.; tibia length 13.7 mm., 50.2 per cent of snout-vent length; foot length (measured from proximal edge of inner metatarsal tubercle to tip of longest toe) 11.7 mm., 42.9 per cent of snout-vent length; head length 8.7 mm., 31.9 per cent of snout-vent length. Snout in lateral profile truncate, rounded above, in dorsal profile rounded; canthus angular; loreal region slightly concave; lips thin, flared. Snout moderately long, distance from anterior corner of eye to nostril slightly less than diameter of eye; nostrils slightly protuberant, directed anterolaterally; internarial area barely depressed; distance between nostrils 2.6 mm.; top of head flat; interorbital distance 3.2 mm., 34.4 per cent of width of head. Diameter of eye 2.7 mm.; thin dermal fold extending from posterior corner of eye to point above insertion of arm; tympanum absent, not visible through skin.

Axillary membrane absent; forearms moderately slender, having indistinct tuberculate fold on ventrolateral edge, lacking distinct transverse fold on wrist; fingers short; length of fingers from shortest to longest, 1-4-2-3, fourth nearly as long as second; discs small, about half again as wide as digits; subarticular tubercules large, round, flattened, distal ones on third and fourth fingers bifid; supernumerary tubercles large, round, present only on proximal segments; prepollex barely enlarged, lacking nuptial excrescence. Web lacking between first and second fingers, extending from base of penultimate phalanx of second to

base of antepenultimate phalanx of third, from middle of antepenultimate phalanx of third to distal end of antepenultimate of fourth finger. Heels overlap by about one-fifth length of shank when hind limbs adpressed; tibiotarsal articulation extending to middle of eye, tarsal fold present, extending full length of tarsus; inner metatarsal tubercle flat, ovoid, partly visible from above; outer metatarsal tubercle absent; toes short; length of toes from shortest to longest, 1-2-3-5-4; discs small, about two-thirds width of those on fingers; subarticular tubercles small, round; supernumerary tubercles small, flattened, irregularly arranged on proximal segments. Toes three-fourth webbed; web extending from base of disc of first to middle of penultimate phalanx of second, from base of disc of second to middle of penultimate phalanx of third, from base of disc of third to base of penultimate phalanx of fourth and to base of disc of fifth toe.

Anal opening directed posteriorly at level of dorsal surfaces of thighs, bordered below by vertical dermal folds and few small tubercles; anal sheath absent. Skin heavily granular on throat, chest, belly and ventral surfaces of thighs, smooth elsewhere. Tongue cordiform, deeply notched posteriorly, barely free behind. Prevomerine teeth 3-4, situated on short elevations between small round choanae; vocal slits absent.

Color (in preservative): pale tan above with dark brown mark in occipital region and large irregular brown mark extending from scapular region to sacral region; anterior and posterior surfaces of thighs and flanks lacking pigment; dorsal surfaces of arms, shanks, and feet tan with brown transverse bars (two on each forearm, two on left shank, one on right shank, and one on each foot); entire dorsal surfaces, except hands and first four toes, peppered with black; venter creamy white; roof of mouth between, and anterior to, choanae speckled with minute black flecks.

Color (in life): yellowish tan above with reddish brown flecks (later changed to pale brown with dull olive-green interorbital bar, blotch on back, and flecks on dorsum); hands, feet, and anterior and posterior surfaces of thighs dull yellow; belly white; creamy white stripes on outer edge of forearm, foot, and above anus; iris pale silver-bronze.

Variation.—Three adult males (including holotype) have snout-vent lengths of 25.2-27.3 (mean 26.5) mm., and two females have 28.6 and 31.6 (mean 30.1) mm. One juvenile has a snout-vent length of 21.5 mm. No significant variation occurs in the proportions. Males have 6-8, and females have 8 and 9, prevomerine teeth. The tympanum is completely concealed in all specimens.

All specimens have distinct transverse bars on the limbs; the number of bars on the shank varies from one to four. Two individuals are dark brown dorsally; in these the small black flecks either are not visible or are absent; flecks are present on the dorsal surfaces of four specimens that are tan or pale brown above with darker brown irregular markings.

The coloration in life consisted of olive-green or olive-brown markings on the body and olive-green or brown bars on the limbs. The dorsal ground color was yellowish tan or pale brown in all individuals.

Comparisons.—*Hyla pellita* differs from all known Middle American *Hyla*, except *mixe, mixomaculata, nubicola,* and *pinorum,* by having a concealed tympanum. The first three of these differ from *pellita* in greater size and by having many bands on the hind limbs. Superficially *H. pellita* resembles *Hyla*

pinorum, which likewise has a tan dorsum with irregular markings and limbs with transverse bars. *Hyla pinorum* differs from *pellita* by having a proportionately larger head, no transverse bands on the thighs, and large tubercles below the anus. Furthermore, in *pinorum* the quadratojugal articulates with the maxillary, whereas in *pellita* the quadratojugal is reduced to a small spur and does not articulate with the maxillary.

Remarks.—All individuals were found on low vegetation along streams in cloud forest at night. No specimens were found when the type locality was revisited in August, 1966.

Duellman (1960) placed *Hyla pinorum* Taylor in the synonymy of *Ptychohyla leonhardschultzei* Ahl. At that time only the holotype, a female, of *H. pinorum* was known. In 1964 Kraig Adler and I independently collected frogs and associated tadpoles in Guerrero that subsequently proved to be *Hyla pinorum* and provided evidence that *Hyla pinorum* is not conspecific with *Ptychohyla leonhardschultzei*.

The specific name *pellita* is Latin, meaning covered with skin, and is here used in reference to the complete concealment of the tympanum beneath the skin.

Hyla siopela new species

Plate 18

Holotype.—Adult male, KU 100981, from a small stream on the west slope of Cofre de Perote, Veracruz, México, elevation 2500-2550 meters; obtained on July 30, 1966, by William E. Duellman.

Paratypes.—KU 100976-80, 100982-5, same locality, date, and collector; KU 105628-9, same locality, obtained on June 18, 1966, by Howard L. Freeman; UIMNH 57687-57701, same locality, obtained on July 30-31, 1964, by Macreay J. Landy and John D. Lynch.

Diagnosis.—A member of the *Hyla bistincta* group characterized by truncate snout with short rostral keel; fingers having little webbing and bearing large discs; axillary membrane absent; thoracic fold weak; prepollex large, flat, bearing small nuptial spines; vocal slits absent; dorsum green or tan with small irregular dark spots; flanks mottled.

Description of holotype.—Adult male having a snout-vent length of 44.3 mm.; tibia length 21.1 mm., 47.6 per cent of snout-vent length; foot length (measured from proximal edge of inner metatarsal tubercle to tip of longest toe) 20.4 mm., 47.2 per cent of snout-vent length; head length 13.4 mm., 30.2 per cent of snout-vent length; head width 13.7 mm., 30.9 per cent of snout-vent length. Snout in lateral profile truncate, in dorsal profile truncate with weak vertical rostral keel; canthus angular; loreal region slightly concave; lips thick, not flaring; snout short; nostrils barely protuberant, directed dorsolaterally, situated about four-fifths distance from anterior corner of eye to tip of snout; internarial distance 3.6 mm.; internarial area not depressed; top of head slightly convex; interorbital distance 4.9 mm., 35.8 per cent of width of head; width of eyelid 3.5 mm., 26.0 per cent of width of head. Diameter of eye 4.7 mm.; heavy dermal fold curving posteroventrally from posterior corner of eye, covering upper one-third of tympanum, to insertion of arm; tympanum barely distinct, its diameter 2.2 mm., 46.8 per cent that of eye, separated from eye by distance equal to half again diameter of tympanum.

Axillary membrane absent; thoracic fold weak; arms moderately robust; fold on wrist heavy; fingers long, slender; length of fingers from shortest to longest, 1-2-4-3; discs large, that on third finger as large as tympanum; subarticular tubercles moderately small, round, none bifid; supernumerary tubercles small, some barely distinguishable, in single row on proximal segment of each digit; prepollex greatly enlarged, flat ventrally, bearing nuptial excrescence composed of minute horny spinules; webbing between first two fingers vestigial; web connecting other fingers at bases of penultimate phalanges of second and fourth, and base of antepenultimate phalanx of third fingers. Heels overlap by about one-third length of shank when hind limbs adpressed; tibiotarsal articulation extends to posterior edge of orbit; transverse dermal fold on heel; tarsal fold thin, distinct, extending length of tarsus; inner metatarsal tubercle large, elongate, flat, visible from above; outer metatarsal tubercle absent; toes moderately long, slender; length of toes from shortest to longest, 1-2-3-5-4; discs slightly smaller than those on fingers; subarticular tubercles moderately small, round; supernumerary tubercles small, in single row on proximal segment of each digit; toes about two-thirds webbed; webbing extends from middle of penultimate phalanx of first toe to base of penultimate phalanx of second, from middle of penultimate of second to middle of antepenultimate of third, from middle of penultimate of third to middle of antepenultimate of fourth to middle of penultimate phalanx of fifth toe.

Anal opening directed posteriorly at level of mid-thigh; anal sheath short. Skin granular on chin, belly, and posteroventral surfaces of thighs, smooth elsewhere. Tongue broadly cordiform, notched posteriorly, barely free behind. Prevomerine teeth 4-4, situated on posteromedially inclined elevations between small ovoid choanae. Vocal slits absent.

Color (in preservative): dull grayish brown above with small, irregularly-shaped black spots on head, back, and limbs; flanks gray mottled with creamy tan; anterior and posterior surfaces of thighs tan; belly dull creamy tan; throat marked with gray blotches; anal region and posterodorsal surfaces of thighs marked with small white spots.

Color (in life): dorsum pale green with black spots and reticulations; flanks mottled dark brown and creamy white; outer edges of feet silvery white with brown spots; anterior and posterior surfaces of thighs dull brown; webbing and first three toes dull yellowish tan; belly creamy gray; throat silvery white, mottled with gray; iris dull bronze-color with black reticulations; palpebral membrane clear.

Variation.—The snout-vent length in seven adult males is 47.2-50.0 mm., and in five females, 45.1-52.5 mm. In neither sex do the average proportions differ noticeably from those of the holotype, except that the tympanum is relatively larger in females. The ratio of the diameter of the tympanum to that of the eye is 0.363-0.468 (mean 0.438) in males and 0.500-0.545 (mean 0.516) in females. The average number of prevomerine teeth in males is 7.9, in females 8.4.

In life dorsal coloration varied from pale green to olive-green with darker green or black flecks or reticulations, or pinkish tan to brown with dark brown flecks or reticulations. Some preserved specimens have relatively few dark flecks, whereas in most specimens the dorsum is heavily marked. All specimens have some white markings above the anus and on the posterodorsal sur-

faces of the thighs, but in some individuals the white flecks are expanded and interconnected forming an irregular white line.

Juveniles have a notably different coloration in life. The dorsum is uniform pale green; the anterior and posterior surfaces of the thighs, fingers, first three toes, and webbing are deep yellow. The anal stripe is creamy white, and the flanks are pale gray with black flecks. The upper lip, supratympanic fold, and canthal stripe are a bronze color. The belly is pale yellow with a silvery cast on the throat. Juveniles having snout-vent lengths from 24.5 to 36.6 mm. are so colored in life, and uniform dark bluish gray dorsally in preservative.

Comparisons.—The absence of a quadratojugal and the presence of a greatly enlarged, non-projecting prepollex place *Hyla siopela* in the *Hyla bistincta* group (see Duellman, 1964, and Adler, 1965). The presence of a rostral keel separates *Hyla siopela* from other members of the *Hyla bistincta* group, which is composed of two species having long anal sheaths (*bistincta* and *pentheter*), two small species having axillary membranes and lacking nuptial excrescences in breeding males (*charadricola* and *chryses*), and three species (*crassa, pachyderma,* and *robertsorum*) having short heads, round snouts, short anal sheaths, and nuptial excrescences in breeding males. *Hyla siopela* differs from the last three species in the shape of the snout and from each in certain structural features; *H. crassa* has fully webbed feet; *H. pachyderma* has large nuptial spines, and *H. robertsorum* has more webbing and a shorter tarsal fold. Furthermore, the venter in *H. robertsorum* is brown with creamy white flecks.

In structure and coloration *H. arborescandens* resembles *siopela,* but the former is smaller, and males of *arborescandens* have vocal slits.

Remarks.—This description brings to eight the number of species now recognized in the *Hyla bistincta* group. *Hyla siopela* is most closely related to *Hyla robertsorum* from the high mountains of the Sierra Madre Oriental in northern Puebla and eastern Hidalgo. Possibly the four species now recognized in the *crassa* subgroup (*crassa, pachyderma, robertsorum,* and *siopela*) are only subspecies of a single species, but differences in the amount of webbing in *crassa* and the nature of the nuptial excrescenses in *pachyderma* indicate that they are distinct species.

The type locality of *Hyla siopela* is a small stream cascading down the western slope of Cofre de Perote; the lower reaches of the stream can be reached by a dirt road leading east from the village of Perote for about 2 kilometers to a small park. The frogs were found in the stream at elevations of 50 to 100 meters higher than the park. The stream flows through a ravine supporting open, dry pine forest. Although the stream was searched thoroughly in February, 1966, no frogs were found. In July, 1966, adults and juveniles were found in crevices and under overhanging rocks behind small cascades and waterfalls by day and sitting on rocks and branches in the spray of cascades at night.

The specific name *siopela* is derived from the Greek *siopelos,* meaning silent, and alludes to the absence of a voice in this species.

Hyla altipotens new species

Plate 19

Holotype.—Adult male, KU 101001, from 37 kilometers (by road) north of San Gabriel Mixtepec (kilometer post 183 on road from Oaxaca to Puerto

Escondido), Oaxaca, México, elevation 1860 meters; obtained on February 19, 1966, by William E. Duellman.

Paratypes.—KU 101002-6 collected at the same locality on February 19 and 20, 1966, by William E. Duellman, and KU 101008 from 33 kilometers (by road) north of San Gabriel Mixtepec, Oaxaca, México, elevation 1675 meters; obtained on February 20, 1966, by Linda Trueb.

Diagnosis.—A member of the *Hyla taeniopus* group characterized by a yellow venter, yellow flecks on posterior surfaces of thighs, bronze-colored stripe from snout, along canthus and edge of upper eyelid to point above arm, pointed snout, smooth dorsum, and no sexual dimorphism in shape of snout.

Description of holotype.—Adult male having a snout-vent length of 68.8 mm.; tibia length 36.2 mm., 52.6 per cent of snout-vent length; foot length (measured from proximal edge of inner metatarsal tubercle) 31.1 mm., 45.2 per cent of snout-vent length; head length 20.2 mm., 29.4 per cent of snout-vent length; head width 20.0 mm., 29.1 per cent of snout-vent length. Snout in lateral profile acutely rounded, protruding beyond tip of lower jaw, in dorsal profile pointed; canthus angular; loreal region flat; lips thick, barely flared. Snout long; nostrils slightly protuberant, directed dorsolaterally, situated about two-thirds distance from anterior corner of eye to tip of snout; internarial distance 5.6 mm.; internarial area slightly depressed; top of head flat; interorbital distance 6.0 mm., 30.0 per cent of width of head; width of eyelid 4.7 mm., 23.5 per cent of width of head. Diameter of eye 6.2 mm.; heavy dermal fold extending from posterior corner of eye, over upper edge of tympanum to point above insertion of arm; tympanum distinct, its diameter 3.4 mm., 54.8 per cent of that of the eye, separated from eye by distance equal to diameter of tympanum.

Axillary membrane absent; arms moderately robust, lacking dermal fold on lateral edge of forearm, having transverse fold on wrist; fingers moderately short, broad; length of fingers from shortest to longest, 1-2-4-3; discs large, that on third finger one-fourth larger than tympanum; subarticular tubercles large, round, none bifid; supernumerary tubercles large, granulelike, present only on proximal segments; prepollex enlarged, not bearing nuptial excrescence. Fingers about one-half webbed; webbing connects first and second fingers at level of distal end of antepenultimate phalanx, extending from middle of penultimate phalanx of second finger to middle of antepenultimate phalanx of third, and between bases of penultimate phalanges of third and fourth fingers. Heels overlap by about one-half length of shank when hind limbs adpressed; tibiotarsal articulation extends to point between eye and nostril; thin transverse dermal fold on heel; tarsal fold strong, extending full length of tarsus; inner metatarsal tubercle small, flat, elongate, barely visible from above; outer metatarsal tubercle small, conical; toes moderately long, stout; length of toes from shortest to longest, 1-2-3-5-4; discs slightly smaller than those on fingers; subarticular tubercles large, round, subconical; supernumerary tubercles large, conical, in single row on proximal segment of each digit; toes about four-fifths webbed; webbing extending from base of disc on first to base of disc on second to base of penultimate phalanx of third toe, from base of disc on third to base of penultimate phalanx of fourth to base of disc of fifth toe.

Anal opening directed posteroventrally at midlevel of thighs; anal sheath long, tubular. Skin smooth on dorsum and on ventral surfaces of shanks,

granular on throat, belly, and ventral surfaces of arms and thighs. Tongue ovoid, widest posteriorly, neither notched nor free behind. Prevomerine teeth 6-7, situated on robust transverse ridges between small, ovoid choanae. Vocal slits absent. Testes large, ovoid, granular; length of left testis 11.0 mm.

Color (in preservative): brown above with many darker brown spots and narrow middorsal stripe on back; six or seven dark brown transverse bars on each segment of hind limbs and four bars on each forearm; flanks white with dark brown spots; anterior surfaces of thighs creamy white with brown reticulations; posterior surfaces of thighs dark brown with creamy yellow flecks; stripe on snout, canthus, edge of upper eyelid, and supratympanic fold tan; ventral surfaces of feet brown; rest of venter creamy white; stripe above anus white.

Color (in life): green above with slightly darker green spots; dorsal surfaces of upper arms and thighs tan with green transverse bars; upper surfaces of forearms and shanks green with darker green transverse bars; feet, fourth and fifth toes, and third and fourth fingers tan with brown transverse bars; other fingers and toes tan with brown flecks. Ventral surfaces creamy yellow, brightest on throat and chest; flanks and anterior surfaces of thighs bright creamy yellow with dark brown reticulations and spots; posterior surfaces of thighs and ventral surfaces of feet dark brown with yellow flecks; ventral surfaces of hands and webbing on hands and feet yellowish tan. Labial stripe tan; stripes on outer edge of forearm, along outer edge of foot, and above anus cream-color; stripe on canthus, edge of upper eyelid, and on supratympanic fold bronze-color. Iris pale bronze with black reticulations and faint median, horizontal copper-colored streak; pupil horizontally elliptical with ventral notch; palpebral membrane clear above, pale bluish green with brown reticulations below.

Variation.—In life all individuals had creamy yellow venters and yellow flanks and anterior surfaces of thighs with brown or black spots and mottling. Most of the adults were colored like the holotype, but one was a much darker olive-green, and one was uniform brown above with a dark brown middorsal stripe. Most subadults (snout-vent lengths 31.6-50.1 mm.) were pale reddish tan above with darker reddish brown bars on the limbs and blotches on the back. The side of the head was dark brown and the stripe along the canthus, edge of upper eyelid, and supratympanic fold was yellowish tan. Some individuals had a dark brown middorsal stripe. The posterior surfaces of the

Table 2.—Variation in Measurements and Proportions in Hyla altipotens. (Means Are Given in Parentheses Below the Observed Range.)

Sex	N	Snout-vent length	Tibia length/ S-V L	Foot length/ S-V L	Tympanum/ eye
Males	5	68.8–75.1 (70.7)	52.6–55.8 (53.7)	28.1–30.0 (29.2)	41.4–55.2 (50.6)
Females	2	69.4–75.3 (72.4)	55.8–56.2 (56.0)	28.8–31.1 (29.9)	53.3–63.0 (58.8)

thighs were dull yellowish tan; yellow flecks were present in the larger individuals.

The number of transverse bars on each thigh and shank varies from five to eight. The white stripe above the anus and the stripe from the snout along the side of the head are invariably present. In some of the largest individuals the brown reticulations on the anterior surface of the thigh extend onto the ventral surface; in these specimens brown flecks are present on the ventral surfaces on the shanks.

The tympanum is proportionately larger in females than in males; the variation in size and proportions is given in Table 2. The total number of prevomerine teeth varies from 13 to 18 (mean, 15) in five adult males and from 10 to 12 (mean 11) in two females.

The testes in all adult males are granular, ovoid in shape, and greatly enlarged. The lengths of the left testis in each of the five males are 11.0 to 23.5 (mean 14.6) mm.

Comparisons.—On the basis of external appearance and certain cranial characters (large frontoparietal fontanelle, broad sphenethmoid, large nasals broadly separated medially having thin lateral processes articulating with the palatines, short squamosal not articulating with the maxillary, and quadratojugal present and articulating with the maxillary), *Hyla altipotens* can be associated with the *Hyla taeniopus* group (Duellman, 1965, Lynch and Smith, 1966). *Hyla altipotens* can be distinguished from all of the other members of the group by its narrow head, pointed snout in both sexes, and uniformly yellow throat and belly.

Small brown individuals of *Hyla altipotens* superficially resemble adult *Hyla pinorum.* The latter species has a covered tympanum, less webbing on the hands, and a short, blunt snout.

Remarks.—This stream-breeding frog is like *Hyla taeniopus* in having greatly enlarged testes, which possibly through the production of vast quantities of sperm are an adaptation for successful breeding in torrential streams (Duellman, 1965:164).

All individuals were found in trees and bushes near streams in cloud forest at night in February. The type locality is the same as that of *Hyla pentheter* and *Hyla thorectes,* discovered by Kraig Adler in June, 1964. Our field work there in February, 1966, resulted in finding *Hyla altipotens, H. pellita,* and *Ptycholyla leonhardschultzei,* but no individuals of the species found by Adler. A visit to the same locality in August, 1966, revealed no individuals of either *H. altipotens* or *pellita;* instead *pentheter* and *thorectes* were found along the stream.

Duellman (1965:166) listed a specimen (TCWC 16184) of *Hyla chaneque* from Los Fustes, 3 kilometers east of San Sebastian, Oaxaca. Reëxamination of this specimen reveals that it is *Hyla altipotens.* The frog was obtained by Dilford Carter on April 29, 1960; it was under a rock at the edge of a stream in an oak-pine-cypress association at an elevation of 1800 meters.

The specific name *altipotens* is Latin, meaning mighty, here used in allusion to the supposed potentiality of fertilization by the production of vast quantities of sperm in the large testes.

Plectrohyla hartwegi new species

Plate 19

Holotype.—Adult male, UMMZ 94428, from Barrejonel (19 kilometers west of Chicomuselo), Chiapas, México, elevation 1000 meters, obtained on June 12, 1941, by Eizi Matuda.

Paratypes.—Two subadult males, KU 58873 from Parajé El Triunfo, north of Mapastepec, Chiapas, México, elevation 2050 meters, obtained on May 12, 1960, by Miguel Alvarez del Toro, and UIMNH 40837 from Cerro Azul Oaxaca, México, obtained on March 7, 1956, by Thomas MacDougall.

Diagnosis.—A *Plectrohyla* having a bifid prepollex, bold mottling on flank and ventral surfaces of shanks, and vertical dark bars on anterior and posterior surfaces of thighs, and lacking vocal slits and outer tarsal fold.

Description of holotype.—Adult male having a snout-vent length of 63.8 mm.; tibia length 34.9 mm., 54.7 per cent of snout-vent length; foot length (measured from proximal edge of inner metatarsal tubercle to tip of longest toe) 31.1 mm., 48.7 per cent of snout-vent length; head length 19.7 mm., 30.9 per cent of snout-vent length; head width 22.6 mm., 35.4 per cent of snout-vent length. Snout short, distance from level of anterior edge of orbit to tip of snout 70.6 per cent of length of eye; snout in lateral profile angular, sloping abruptly from nostrils to jaw, in dorsal profile bluntly rounded, lacking rostral keel; canthal ridge thickened; loreal region deeply concave; lips thick, barely flared. Nostrils small, barely protuberant, directed anterolaterally, situated about two-thirds distance from eye to tip of snout; internarial distance 5.6 mm. internarial area barely depressed near convergence of canthal ridges; top of head flat; interorbital distance 6.4 mm., 28.3 per cent of head width; diameter of eye 6.8 mm.; width of eyelid 5.5 mm., 24.3 per cent of head width. Heavy dermal fold extending posteriorly from posterior edge of orbit, covering upper edge of tympanum; two thinner folds extending ventrally from longitudinal heavy fold covering posterior edge of tympanum; anterior and ventral edges of tympanum distinct; length of tympanum 2.9 mm., 42.6 per cent of diameter of eye.

Axillary membrane absent; arms robust, forearm not noticeably heavier than upper arm; distinct transverse fold on wrist. Fingers long, moderately slender; length of fingers from shortest to longest, 1-2-4-3; discs moderately large, that on third finger larger than tympanum; webbing vestigial; subarticular tubercles small, conical; terminal tubercle on fourth finger somewhat flattened; supernumerary tubercles small, in one row on proximal segment of fourth finger and in two rows on proximal segments of other fingers; prepollex greatly enlarged, barely bifurcate; spines not protruding through skin; distal spine much longer than proximal one (Fig. 2). Heels overlap by about one-third length of shank when hind limbs adpressed; tibiotarsal articulation extends slightly beyond snout; heavy transverse dermal fold on heel; inner tarsal fold heavy, extending full length of tarsus; outer tarsal fold absent; inner metatarsal tubercle high, elliptical, visible from above, outer metatarsal tubercle absent. Toes long, slender; length of toes from shortest to longest,

Fig. 2. Palmar view of prepollical spine of right hand of *Plectrohyla hartwegi* (UMMZ 94428). ×5.

1-2-5-3-4; fifth toe nearly as long as third; discs small; subarticular tubercles small, round; supernumerary tubercles small, in single row on proximal segment of each digit; toes about three-fourths webbed; webbing extending from base of disc of first toe to base of penultimate phalanx of third, from base of disc of third to base of penultimate phalanx of fourth to base of disc of fifth toe.

Anal opening directed posteroventrally at level of mid-thigh; anal sheath long with membranous connection to posterior surfaces of thighs. Skin on dorsal surfaces finely tuberculate; that on throat, chest, belly, and ventral surfaces of thighs granular, that on ventral surfaces of arms and shanks smooth. Tongue nearly round, free posteriorly for about one-fourth its length, barely notched behind. Upper jaw shallowly notched medially. Maxillary-premaxillary teeth 38-35; prevomerine teeth 5-5, situated on small elliptical elevations between quadrangular choanae; vocal slits absent.

Color (in preservative): uniform dull brown above and creamy yellow below; flanks brown with creamy yellow mottling and dark brown spots in groin; anterior surfaces of thighs creamy yellow with two broad, vertical, dark brown bars proximally and two narrower, dull brown bars distally; posterior surfaces of thighs brown with dark brown vertical bars, interspaces cream-colored or brown. Ventral surfaces of shanks creamy yellow with bold brown reticulations.

Variation.—The paratypes are smaller, having snout-vent lengths of 48.3 and 41.8 mm. In these specimens the ratio of the length of the tibia to the snout-vent length is 55.9 and 57.9 per cent, and the ratio of the diameter of the tympanum to the diameter of the eye is 47.3 and 43.6 per cent, respectively. Both specimens have 4-4 prevomerine teeth; one specimen has 37-36, and the other has 40-37, maxillary-premaxillary teeth. In these small specimens the supratympanic fold is thin, and the arms are not so robust as in the holotype. In one specimen (KU 58873) the tongue is not notched posteriorly. The terminal subarticular tubercle on each fourth finger is broad and flattened in UIMNH 40837, but conical in KU 58873. Both specimens have bold creamy-yellow and dark brown mottling on the flanks and dark brown reticulations on the ventral surfaces of the shanks. There are two dark brown vertical bars on the anterior and posterior surfaces of each thigh in KU 58873 and three bars on each surface in UIMNH 40837.

Comparisons.—*Plectrohyla hartwegi* differs from all known species in the genus by having boldly mottled flanks, dark reticulations on the ventral surfaces of the shanks, and dark vertical bars on the shanks. In all of the other species the anterior and posterior surfaces of the thighs are unmarked, and the flanks are either plain or marked with small spots or flecks. Structurally, *P. hartwegi* belongs in the *guatemalensis* group of the genus, containing *avia, glandulosa, guatemalensis,* and *pycnochila.* The species in this group lack vocal slits and have either large, rectangular, or bifid prepollices. *Plectrohyla hartwegi* differs from all of these species, except *pycnochila,* by having a tuberculate, instead of a smooth, dorsum, and *hartwegi* differs from *pycnochila* by having a bifid, instead of a rectangular, prepollex.

Remarks.—The known distribution of *Plectrohyla hartwegi* includes three localities at elevations of 1000 to 2050 meters in the Sierra Madre of Chiapas and extreme eastern Oaxaca. The specimen from Parajé El Triunfo was found in a rocky stream in cloud forest at an elevation of 2050 meters. One *Plectrohyla sagorum* was obtained from the same stream.

Eizi Matuda sent the holotype to the late Dr. Norman Hartweg, who recognized that the specimen was unique but was reluctant to name the species on the basis of a single specimen. Now that two additional specimens are available, it seems appropriate to associate Hartweg's name with this new species of *Plectrohyla*, a genus that Hartweg first adequately defined.

LITERATURE CITED

Adler, K.

1965. Three new frogs of the genus *Hyla* from the Sierra Madre del Sur of México. Occas. Papers Mus. Zool. Univ. Michigan, 642:1-18, pl. 1, December 16.

Duellman, W. E.

1960. Synonymy, variation, and distribution of *Ptycholuyla leonhardschultzei* Ahl. Studies of American hylid frogs, IV. Herpetologica, 16:191-197, September 23.

1964. A review of the frogs of the *Hyla bistincta* group. Univ. Kansas Publ. Mus. Nat. Hist., 15:469-491, March 2.

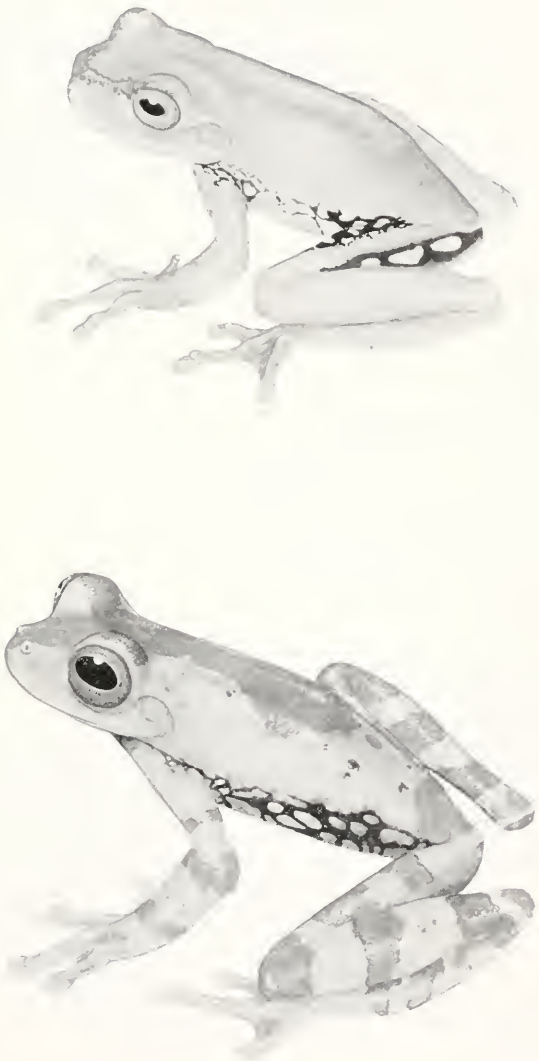
1965. Frogs of the *Hyla taeniopus* group. Copeia, 2:159-168, June 25.

Starrett, P.

1966. Rediscovery of *Hyla pictipes* Cope, with description of a new montane stream *Hyla* from Costa Rica. Bull. South. California Acad. Sci., 65 (1):17-28, March.

Transmitted July 11, 1967.

PLATE 17



Upper figure, *Hyla xanthosticta* (KU 103772); lower figure, *Hyla pseudopuma infucata* (KU 101770). × 2.

PLATE 18

Upper figure, *Hyla pellita* (KU 100973); middle figure, *Hyla pellita* (KU 100970); lower figure, *Hyla stopela* (KU 100977). × 2.

PLATE 19

Upper figure, *Hyla altipotens* (KU 101001); lower figure, *Plectrohyla hartwegi* (UMMZ 94428). × 1.

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Summer Birds From the Yucatan Peninsula, Mexico

BY

ERWIN E. KLAAS

University of Kansas
Lawrence
1968

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Summer Birds From the Yucatan Peninsula, Mexico

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INTRODUCTION

Because its unique geographical location and ecological setting supports a rich and varied avifauna, the Yucatán Peninsula has received considerable attention by ornithologists. The most valuable contribution is Paynter's "The Ornithogeography of the Yucatán Peninsula" (1955a), an authoritative study of the composition, distribution, and origin of the avifauna of the region. His work contains a complete listing of all species reported to that time from the peninsula. It considers the hundreds of specimens collected by the author and his associates during many months of field work, provides a synthesis of all the information available to 1955, and is the basic reference to the avifauna of the area. Paynter also pointed out matters for which information is lacking. Two of the most conspicuous deficits that he noted are the lack of knowledge about many species that occur on the peninsula in summer, and the paucity of data as to time of breeding, although some information on reproduction in a few species was published subsequently by Paynter (1955b) and Storer (1961).

In July and August of 1962, I was a member of a field party from the Museum of Natural History, The University of Kansas, engaged in a survey of vertebrates and their ectoparasites on the Yucatán Peninsula. The purpose of the present paper is to report on the birds collected and observed during the course of this field work. Particular emphasis is given to breeding information, but observations concerning distribution, incidence, and molt also are given. In addition, a list of the chewing lice (Mallophaga) taken from various specimens is given in Table 2 and in the appropriate species account of the host. Other ectoparasites removed from these birds will be reported on elsewhere.

ACKNOWLEDGMENTS

I am especially indebted to Dr. J. Knox Jones, Jr., under whose direction this field study was undertaken, and to Dr. Richard F. Johnston who aided greatly in the identification of specimens and critical reading of the manu-

script. I am grateful also to other members of the field party who helped in collecting many of the specimens reported herein: Ticul Alvarez, A. Binion Amerson, Dr. William E. Duellman, Dr. J. Knox Jones, Jr., Thomas E. Lovejoy, III, Jack G. Makepeace, Dwight R. Platt, William C. Stanley, Jerome B. Tulecke, and John Wellman. Dr. K. C. Emerson graciously identified the specimens of Mallophaga and Dr. Allan R. Phillips aided in identification of some of the birds.

In addition, I wish to express sincere thanks for quarters provided our field party at the Campo Experimental Forestal "El Tormento" at Escárcega, Campeche, by Ing. Hector Flores S.; at Pueblo Nuevo X-can, Quintana Roo, by Pablo Alimilla; at Felipe Carrillo Puerto, Quintana Roo, by Fernando Esquival Montono; and at Pisté, Yucatán, by Luis V. Polanco. The field party benefited also from arrangements and helpful suggestions made by Eduardo C. Welling of Mérida and Marynoll Father Joseph Early of Felipe Carrillo Puerto. Wherever we camped the local Mayans were exceptionally helpful, especially as guides and collectors.

Our field party was composed of two units. One unit, working on a survey of Middle American vertebrates and their ectoparasites, was supported by the United States Army Medical Research and Development Command (Contract No. DA-49-193-MD-2215). The second unit, composed of students in the Field Course in Vertebrate Zoology from The University of Kansas, was supported in part by the Museum of Natural History and by a grant from the National Science Foundation (G 20939, Special Projects in Science Education). The late Ing. Luis Macías Arellano, Departamento de la Fauna Silvestre, Dirección General de Caza, México, D. F., generously provided the necessary permits for collecting vertebrates.

PHYSICAL FEATURES

The Yucatán Peninsula is a northeastern projection of Central America lying between the Gulf of Campeche, the Gulf of Mexico, and the Caribbean Sea. Its area is approximately 143,500 square kilometers and includes the Mexican states of Campeche and Yucatán and the sparsely settled Territory of Quintana Roo, plus parts of British Honduras and the Petén region of Guatamala. The peninsula has a mean breadth of about 300 kilometers and a coast line of about 1100 kilometers.

Topographically, the peninsula is a low-level plain that rises gradually inland to the south. The coast on the north and west is low, sandy, and semibarren; openings through the outer coastal strand lead to narrow brackish lagoons surrounded by mangroves. The eastern coast consists of bluffs, indented with bays and bordered by several islands, the largest being Cozumel. A small range of hills traverses the peninsula from the city of Campeche to Chetumal Bay; although appearing sizeable, these almost nowhere exceed 100 meters in elevation. The extreme southerly portion of the peninsula is moderately hilly and is covered with tropical rain forest.

The peninsula is composed almost wholly of a bed or coraline and porous limestone covered with a layer of thin, dry soil formed from the slow weathering of the bedrock. The humus is rarely more than a few centimeters deep, and consequently cornfields (*milpas*) must be moved every two or three years. With each move a new area of the land is cleared and burned. This agricultural

practice has been routine with the Mayan people for centuries and apparently has had a profound effect on the vegetation, severely limiting the extent of virgin forest.

In many places, especially in the northern part of the peninsula, the rocky surface of the terrain is perforated by natural wells or sink-holes, which are called *cenotes* locally. Many *cenotes* support small "islands" of unique vegetation, the composition of which somewhat resembles the rain forest of the southern part of the peninsula. Temporary water-holes and shallow lakes (*aguadas*) are sparsely scattered throughout the southern half of the peninsula. There are no rivers of importance; most that are present are in the southernmost region.

The climate of northern Yucatán is hot and dry, and the absence of high mountainous ridges to intercept the moisture-bearing clouds from the Atlantic accounts for less rain than would be expected. The southernmost part of the peninsula receives a maximum of 200 centimeters of rain annually. The amount decreases toward the north to an average of about 45 centimeters. Almost all of the rain falls from May to October. Daily temperatures range from 78° to 98° F. in the shade; cool sea winds prevail day and night throughout most of the year. The hottest months are May and June. In winter, fierce northers, *temporales* or *nortes*, occasionally sweep across this open region, bringing rain and cooler temperatures, lasting several days.

The areas adjacent to British Honduras and Guatemala receive sufficient rainfall to support forests containing mahogany (*Swietenia*); sapodilly (*Achras*); several valuable cabinet woods; logwood (*Haematozylon*) and other dyewoods. As one proceeds northward the flora and fauna change gradually from that of the wet tropics to that of the dry tropics.

Paynter's (1955a) system of vegetational zones on the peninsula is useful to ornithologists. He recognized three zones: Scrub, Deciduous Forest, and Rain Forest. The Scrub zone occupies Isla Holbox and Isla Mujeres and the arid northern coast of Yucatán. The zone extends only a few miles inland and consists of low-tropical thorn forest of mesquite (*Prosopsis*), *Mimosa, Yucca, Agave,* and mangrove (*Rhizophora*) wherever standing water occurs. Sisal in Yucatán and Isla Mujeres of Quintana Roo are in this Scrub zone.

The Deciduous Forest zone is a vast area of low, semiarid, secondary forest occupying all of the state of Yucatán not in the Scrub zone, northern Campeche, and a thin strip a few kilometers wide in Quintana Roo along the Yucatán-Quintana Roo border and a similar narrow band along the eastern coast. The island of Cozumel is also included in this zone. Collections were made in the Deciduous Forest at Champotón, Campeche, Isla Cozumel and Puerto Juárez, Quintana Roo, and Pisté, Yucatán.

The Rain Forest zone occupies the remainder of the peninsula and includes most of the territory of Quintana Roo, and the southern half of Campeche. Collections were made in this zone at Escárcega, Campeche, and at Felipe Carrillo Puerto and Pueblo Nuevo X-can, Quintana Roo. Isla del Carmen cannot be accurately assigned to any of these three zones because most of the island has been planted in coconut palms. It is an area of high rainfall and may once have supported rainforest.

In the present report the term "second growth" refers to areas that have been recently cut over. In these areas, the forest is characteristically low and in a

stage of transition. In the Rain Forest zone "second growth" areas usually contain species of deciduous trees.

Paynter (1955a) has given an excellent descriptive summary of the topography, climate, and phytogeography of the Yucatán Peninsula and there is little need to go into further detail here. During summer, the rainy season, the Deciduous Forest is much more luxuriant in appearance than in winter when most of the trees have lost their leaves. Also, the numerous *cenotes* in this zone support a limited growth of evergreen trees. For example, the large Cenote Seco about two kilometers east of Chichén-Itzá contains elephant ear (*Caladium*), mamey (*Mammea*), figs (*Ficus*), and other large trees the trunks of which are some 10 meters below the surface of the surrounding tableland. These plants project five to 10 meters above the surrounding low forest. The floor of this *cenote* is near the watertable but not below it.

GAZETTEER

The specimens of birds reported herein were collected at the localities shown on the accompanying map (Fig. 1). These localities are listed below in alphabetical order according to states.

Campeche

Champotón.—Lat. 19° 21′ N, long. 90° 43′ W, sea level to five meters. A fishing village on the Gulf of Mexico. Collections were made principally at our camp five kilometers south of the town. Low deciduous forest, second growth, and *milpas*.

Escárcega.—Lat. 18° 37′ N, long. 90° 44′ W, elevation 65 meters. A village in southwestern Campeche. Field work was carried out principally in the vicinity of an agricultural experiment station seven and a half kilometers west of the town. Second growth and moderately tall rainforest.

Isla del Carmen.—Lat. 18° 43′ N, long. 91° 41′ W, sea level to two meters. An island in the mouth of Laguna de Términos. Collections were made at our camp on the northeastern end of the island, about one kilometer southwest of Puerto Real. Coconut plantations and mangrove swamp.

Quintana Roo

Felipe Carillo Puerto.—Lat. 19° 35′ N, long. 88° 02′ W, elevation 30 meters. A village in east-central Quintana Roo. Field work was centered at Rancho San Miguel, about four kilometers north-northeast of the village. Mostly second growth rainforest with scattered large patches of tall trees (to 30 meters). Several large *milpas* were present on the ranch some of which had been recently cleared. Our camp was at a large aguada bordered on one side by an extensive marsh with tall dense grass.

Isla Cozumel.—Lat. 20° 27′ N, long. 86° 26′ W, sea level to 10 meters. A large island, 15 kilometers east of the mainland. Collections were made on the northwestern part of the island from one to five kilometers north-northeast of the village of San Miguel in low, dense deciduous forest.

Isla Mujeres.—Lat. 21° 12′ N, long. 86° 43′ W, sea level to 30 meters. A small, narrow island about eight kilometers from the coast at the northeastern end of the peninsula. Field work was done on the beach at the northern end of the island, in low deciduous forest in the middle of the island, and in low deciduous forest and cactus (*Opuntia*) association on a high rocky bluff on the southern end of the island.

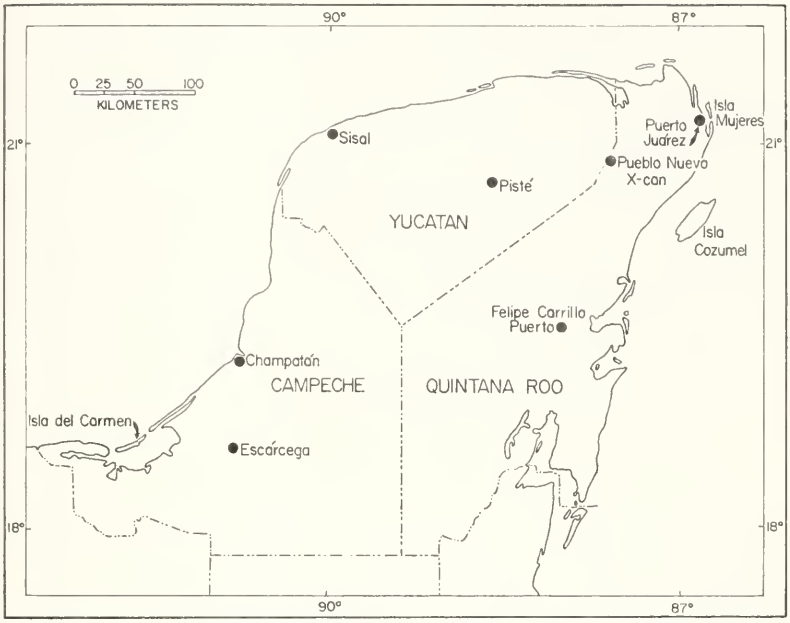

FIG. 1. A map of the Yucatán Peninsula of Mexico showing localities referred to in the text.

Pueblo Nuevo X-can.—Lat. 21° 52′ N, long. 87° 26′ W, elevation 10 meters. A village five kilometers east of X-can, Yucatán, in rainforest with dense underbrush. Specimens were obtained from the immediate vicinity of the village.

Puerto Juárez.—Lat. 21° 10′ N, long. 86° 49′ W, sea level. A small port on the Caribbean Coast with alternating sand beach and limestone shore. Mangrove swamps extend a short distance inland at various points. Specimens were collected in rainforestlike vegetation at a small *cenote*, in low deciduous forest, and at our camp along a large, cleared airstrip four kilometers west-southwest of the village.

Yucatán

Pisté.—Lat. 20° 42′ N, long. 88° 28′ W, elevation 10 meters. A village in dense, low deciduous forest with many nearby *milpas*. Collections were made in a wide area in the vicinity of the village, including nearby Chichén-Itzá.

Sisal.—Lat. 21° 10′ N, long. 90° 00′ W, sea level. A small village on the northwestern coast of the peninsula. Collections were made on the beach, in the low scrub vegetation behind the beach, and in the mangrove swamps and nearly-dry lagoons further inland, from three to 13 kilometers west-southwest of the village.

ANNOTATED LIST OF SPECIES

Catalogue numbers in the following accounts are those of the Museum of Natural History, The University of Kansas. With the exception of a synoptic collection presented to the Departamento de la Fauna Silvestre, Dirección

General de Caza, México, D. F., all of the specimens mentioned are in the museum at the University of Kansas.

Unless otherwise indicated, specimens taken were not molting. For birds undergoing postnuptial or postjuvenal molt, the degree of advancement of the molt is indicated by the numbers of primaries and rectrices that are new or partly ensheathed. Information on the condition of the testes refers to the left testis unless otherwise noted.

Scientific and vernacular names follow Friedmann *et al.* (1950) and Miller *et al.* (1957) except for specimens of species or genera that have been more thoroughly treated systematically since the publication of the Mexican Checklist, for example, *Columbina, Centurus* and *Platypsaris*, by Johnston (1962), Selander and Giller (1963), and Webster (1963), respectively. The trinomial is used whenever subspecific identities could be made with a reasonable degree of certainty. The specimens of several kinds were in extremely worn plumage or in molt and meaningful judgments concerning such characters as relative darkness or paleness of plumages could not be made.

Specimens are listed in each account according to the temporal order in which they were collected.

Bulbulcus ibis Linnaeus: Cattle Egret.—Our specimen is one of three individuals seen feeding near cattle at Rancho San Miguel on August 13 and 14.

Specimen (1): ♂, 40401, testis 6 x 2 mm., 289.5 gm. (August 14), 4 km. NNE Felipe Carrillo Puerto.

Casmerodius albus (Linnaeus): American Egret.—We took one egret from a flock of about 20 that flew low over our campsite on the morning of July 12.

Specimen (1): ♀, 40402, ovary inactive, 10 x 5 mm., 607.5 gm. (July 12), 5 km. S Champotón. Mallophaga: *Ciconiphilus obscurus.*

Cochlearius cochlearius (Linnaeus): Boat-billed Heron.—Three individuals were seen on a small point of land immediately south of the village on the west coast of Isla Mujeres on the afternoon of August 1. One was foraging in a small cove about one mile south of the village on the morning of August 2. Paynter (1955a) did not list the species for Isla Mujeres; our observations seem to constitute the first records for the island.

Mycteria americana Linnaeus: Wood Ibis.—A flock of about 15 flew over our camp 4 km. NNE Felipe Carrillo Puerto on August 14.

Sarcoramphus papa (Linnaeus): King Vulture.—Our specimen was one of two individuals seen at a cenote.

Specimen (1): ♂ 40403, testes inactive, 8 lbs. (July 29), 1 km. N Pueblo Nuévo X-can. Mallophaga: *Colpocephalum megalops.*

Carthartes burrovianus Cassin: Yellow-headed Vulture.—We saw several Yellow-headed Vultures on Isla del Carmen on July 6, 7, 8, and 9. *C. burrovianus* was more abundant than either *Carthartes aura* or *Coragyps atratus* in the vicinity of Champotón, where we confirmed field identifications by taking a specimen. Until Wetmore (1950) clarified the status of *C. burrovianus* in southern Mexico and Central America, the species had gone unnoticed or misidentified as *C. aura.* The Mexican Checklist (Friedmann, Griscom, and Moore, 1950) omitted *C. burrovianus* from the avifauna of México. Blake (1953) included Tabasco, Chiapas, and Veracruz within the range of the species, but

Paynter (1955a) omitted it from his list of birds of the Yucatán Peninsula. Our specimen seemingly constitutes the first record from the peninsula.

Specimen (1): ♂, 40404, testes inactive, 1¾ lb. (July 9), 2 km. S Champotón.

Chondrohierax uncinatus uncinatus (Temminck): Hook-billed Kite.—A pair was seen 5 km. S Champotón on July 8 and 9. Both birds were in adult plumage and appeared to be mated, although we found no nest. The male is referable to *C. u. uncinatus* on the basis of the narrow white ventral bands, most of which are 0.3 millimeter or less in width. None of the bars exceeds 0.5 millimeter in width. Paynter (1955a) discussed in detail the contradictions in the literature concerning the geographic range of this subspecies, and referred a male in his collection taken in February, 1952, to *C. u. aliquonis*. Traylor (1941) collected a large series of this species in Yucatán and Campeche in winter and allocated the specimens to the nominate form.

At Pisté, on July 23, a nestling approximately half-grown was brought in by a local boy. The rectrices were partly ensheathed and the feather count extensively downy.

Specimens (2): ♂, 40406, testis 9 x 5 mm., 215.0 gm. (July 10), 5 km. S Champotón; ♂, 40405, nestling, 117.6 gm. (July 24), Pisté.

Buteo magnirostris gracilis (Ridgway): Roadside Hawk.—This was the only hawk seen on Isla Cozumel.

Specimens (2): ♂, 40411, testis 5 mm., 207.3 gm. (August 10), 4 km. N San Miguel; ♀, 40412, 242 gm. (August 10), 3½ km. N San Miguel.

Buteo magnirostris conspectus (Peters): Roadside Hawk.—This species was the commonest hawk on the peninsula and was seen at all localities except Isla Mujeres and Sisal.

Specimens (5): ♂, 40409 (July 12), and ♀, 40410, ova to 1 mm., 249 gm. (July 16), 7½ km. W Escárcega; ♂, 40413, 279 gm. (July 17) 1 km. N, 13 km. W Escárcega; ♂, 40407, testis 5 x 2 mm., 254.7 gm. (July 23), Pisté: ♀, 40408, ovary inactive, 279.0 gm. (July 28), Pueblo Nuevo X-can.

Buteo brachyurus Vieillot: Short-tailed Hawk.—Our one specimen, a male (40414) weighing 342 gm. and in white-bellied phase, was taken by a native 6 km. W Escárcega on July 14. The testes were inactive.

Buteo nitidus plagiatus (Schlegel): Gray Hawk.—Our specimen is one of two subadults sighted near a large *milpas,* on Rancho San Miguel.

Specimen (1): ♂, 40415, testis 5 x 3 mm., 364 gm. (August 15), 4 km. NNE Felipe Carillo Puerto. Mallophaga: *Craspedorrhy* sp.

Buteogallus anthracinus (Lichtenstein): Common Black Hawk.—Five individuals were seen on August 23 along a stretch of five miles of highway about 30 mi. SW Champotón, Campeche. The species was identified from the description given in Blake (1953). The hawks were perched on dead limbs in full view, 50 to 100 feet from the highway, which at this locality parallels the beach, sometimes only a few yards from the water.

Ortalis vetula intermedia Peters: Chachalaca.—Chachalacas were heard or seen at all localities on the mainland except Sisal.

Specimens (3): ♀, 40416, 423 gm. (July 13), ♀, 40417, 432 gm. (July 15), and ♀, 40418, ovary 12 x 9 mm., 408.5 gm. (July 16), 7½ km. W Escárcega. Mallophaga: *Amyrisidea spicula,* July 16.

Colinus nigrogularis persiccus Van Tyne and Trautman: Black-throated Quail.—These quail were abundant in the arid scrub west of Sisal. Several coveys of half-grown chicks were seen and specimens taken were in full breeding condition. On a two-mile walk on August 18, in the coastal scrub about 5 km. W Sisal, a pair of quail was seen about every 100 paces.

Specimens (4): ♀, 40422, ovum in oviduct 30 x 22 mm., 147.5 gm. (August 10), ♀, 40420, ovum in oviduct 27 mm., 151.7 gm. (August 18), ♂, 40421, testis 9 x 5 mm., 119.6 gm. (August 18), and ♂, 40419, testis 11 x 6 mm., 145.7 gm. (August 18), all from southwest of Sisal.

Laterallus ruber (Sclater and Salvin): Little Red Rail.—Two specimens were taken about 3½ km. N San Miguel, Isla Cozumel, in tall grass. One bird was shot when flushed; the other was caught in a Museum Special mousetrap. I follow Brodkorb (1943) and Paynter (1955a) who did not recognize subspecies in this species.

Specimens (2): ♀, 40424, ovary 9 x 3 mm., 41.5 gm. (August 8), and ♂, 40423, testis 6 mm., 40.0 gm. (August 11), Isla Cozumel.

Porphyrula martinica (Linnaeus): Purple Gallinule.—A female was taken in the tall grass where red rails were found on Isla Cozumel.

Specimen (1): ♀, 4025, ovary 14 x 7 mm., 169 gm. (August 10), 3½ km. N San Miguel.

Haematopus ostralegus Linnaeus: Oyster-catcher.—Two individuals were seen along the beach about 6 km. W Sisal on August 10 and 11.

Charadrius alexandrinus tenuirostris (Lawrence): Snowy Plover.—This was one of the commonest shorebirds on the beaches and mudflats west of Sisal. Several immature birds were taken, along with a pair of half-grown chicks, indicating the species was breeding, or recently had bred, there. No previous record of this species breeding on the peninsula has been found.

Specimens (6): ♀, 40431, ovary inactive, 38.2 gm. (August 7), 4 mi. S Sisal; ♂, 40426, testis minute, 35.4 gm. (August 9), ♀, 40427, half-grown chick, 25.4 gm. (August 9), ♂, 40428, half-grown chick, 21.2 gm. (August 9), ♀, 40430, imm., 38.0 gm., little fat (August 10), ♀, 40429, ovary inactive, 35.7 gm., little fat, molting—1st through 6th primaries and middle pair of rectrices are new (August 10), all from 13 km. WSW Sisal. Mallophaga: *Actornithophilus ochraceus,* August 9; *Quadraceps assimilis major,* August 7.

Charadrius wilsonia wilsonia Ord: Wilson Plover.—A flock of about 11 was seen on the beach north of the village on Isla Mujeres on August 1. Two specimens were collected on the leeward side of the island about three kilometers south of the village on August 2. The only evidence of breeding was slightly enlarged testes in one male. Two individuals were sighted on the east coast of the mainland at Puerto Juarez on August 4. The species was common 3 to 13 km. west-southwest of Sisal; specimens taken there may have been migrants.

Specimens (5): ♂, 40435, testis 3 x 1 mm., 59.0 gm. (August 2), and ♀, 40436, ovary inactive, 49.3 gm. (August 2), Isla Mujeres; ♀, 40434, ovary inactive, 53.6 gm. (August 7), ♂, 40433, testis 1 mm., 54.5 gm. (August 9), and ♂, 40432, imm., 53.7 gm., little fat (August 11), 3-13 km. WSW Sisal. Mallophaga: *Quadraceps assimilis major,* August 2 and August 11.

Actitis macularia (Linnaeus): Spotted Sandpiper.—A total of six individuals was seen on Isla Mujeres; each was alone. The species was common at Sisal where it was often seen in small mixed flocks with Snowy Plovers and Wilson Plovers.

Specimens (3): ♂, 40437, testis 2 x 1 mm., 33.8 gm. (August 9), ♂, 40438, imm., 28.2 gm. (August 10), and sex? 40439, imm., 31.0 gm. (August 10), 13 km. WSW Sisal. Mallophaga: *Quadraceps ravus;* August 10.

Catoptrophorus semipalmatus inornatus (Brewster): Willet.—A flock of 15 or 20 individuals was seen almost every day of our stay on the beach 8-13 km. WSW of Sisal. Measurements of two of the specimens are large and they are clearly referable to *C. s. inornatus.*

Specimens (3): ♂, 40441, testis 3 mm., 242.3 gm., wing 205 mm., tail 80 mm., tarsus 66 mm., culmen (from feathers) 60 mm. (August 9), ♀, 40440, ovary inactive, 240.5 gm., wing 204 mm., tail 77 mm., tarsus 69 mm., culmen (from feathers) 59 mm. (August 11), and ♂, 40442, imm., 221.1 gm. (August 11) 8-13 km. WSW Sisal. Mallophaga: *Austrominopon sachlebeni,* August 9; *Quadraceps carrikeri,* August 11.

Arenaria interpres (Linnaeus): Turnstone.—Six individuals were sighted on Isla Mujeres on August 1 and one individual was sighted 4 km. W Sisal on August 11.

Crocethia alba (Pallas): Sanderling.—This species was relatively common at Sisal where several flocks of 30 to 40 birds were seen. One specimen (40444) shows an unusual pattern of molt; replacement of outer primaries has preceded that of the inner.

Specimens (4): ♂, 40445, testis 3 x 1 mm., 57.5 gm., heavy fat (August 9), ♀, 40444, ovary granular 6 x 3 mm., 56.7 gm., molting (August 11), ♂, 40443, 35.5 gm. (August 11), and ♀, 40446, imm., 54.1 gm. (August 11), 6½-13 km. WSW Sisal. Mallophaga: *Lunaceps holophaeus actophilus,* August 11; *Carduiceps zonarius,* August 11.

Ereunetes pusillus (Linnaeus): Semipalmated Sandpiper.—The only individual seen was taken from a mixed flock of Sanderlings and Wilson Plovers.

Specimen (1): ♂, 40447, testis minute, 24.4 gm. (August 11), 8 km. WSW Sisal.

Himantopus mexicanus (Müller): Black-necked Stilt.—A lone individual was sighted on Isla Mujeres on August 2. A pair was on the mudflats among mangroves at Sisal, of which the male was taken on August 7. Although Paynter (1955a) indicated that this species probably breeds on the peninsula, there are no definite breeding records. Our specimen had only slightly enlarged testes, but its close association with a female suggested that the pair may have been mated.

Specimen (1): ♂, 40448, testis 7 x 3 mm., 189.4 gm., little fat (August 7), 5 mi. SW Sisal.

Larus atricilla Linnaeus: Laughing Gull.—This species was seen regularly along the coasts of the peninsula.

Specimen (1): ♀, 40449, ovary 7 mm. (inactive), 253 gm. (August 7), 4 3/10 mi. W Sisal. Mallophaga: *Quadraceps* sp.

Sterna albifrons antillarum (Lesson): Least Tern.—A flock of about 20 individuals was seen on Isla Mujeres; two individuals were shot and appear to be the first specimens from the island.

Specimens (2): ♀, 40451, ovary slightly enlarged, 49.0 gm. (August 2); sex? 40450, 41.8 gm. (August 2), Isla Mujeres.

Thalasseus sandvicensis (Latham): Cabot Tern.—Lone individuals were seen several times flying along the coast southwest of Sisal.

Specimen (1): ♂, 40452, 186 gm. (August 11), 13 km. WSW Sisal. Mallophaga: *Saemundssonia brevicernis.*

Patagioenas flavirostris flavirostris (Wagler): Red-billed Pigeon.—This species was seen at all stations except on the islands and in the arid scrub at Sisal. It was especially abundant at Escárcega, Felipe Carrillo Puerto, and Puerto Juarez. The male in breeding condition suggests that the breeding season extends into the summer.

Specimens (5): ♀, 40455, ovary inactive (July 13), ♀, 40456, ovary inactive, (July 13), and ♂, 40457, testis 7 x 5 mm. (July 15), 6-7½ km. W Escárcega; ♂, 40453, testis 15 x 6 mm., 225.5 gm. (August 16), and ♀, 40454, ovary inactive, 228 gm. (August 16), 4 km. NNE Felipe Carrillo Puerto. Mallophaga: *Columbicola* sp., July 15.

Zenaida aurita yucatanensis Salvadori: Zenaida Dove.—This species was common at Sisal.

Specimens (3): ♀, 40459, imm., 136.5 gm., little fat (August 11), 8 km. SW Sisal; ♀, 40399, 151.2 gm. (August 7), 1½ mi. S Sisal; ♀, 40400, 163.3 gm. (August 18), 2 km. WSW Sisal. Mallophaga: *Columbicola macrouras*, August 7.

Zenaida asiatica Linnaeus: White-winged Dove.—Birds of this species were ubiquitous in the scrub west of Sisal between 10 a. m. and 4 p. m. but inconspicuous at other times. Apparently the birds were from nests, roosts, and watering sites in the taller forest inland.

Columbina passerina pallescens (Baird): Common Ground Dove.—This species was common at almost all collecting localities, but was always outnumbered by the Ruddy Ground Dove. The species was not seen in the vicinity of Escárcega, probably because of the tall forest and lack of clearings there.

Specimens (5): ♂, 40461, testis 10 x 5 mm., 40.9 gm. (August 10), 2 km. WSW Sisal; ♂, 40460, testis 6 x 3 mm. (August 9), and ♀, 40464, ova to 4 mm., 37 gm. (August 9), 3½-4 km. N San Miguel, Isla Cozumel; ♀, 40463, imm., molting, 35.5 gm. (August 15), 4 km. NNE Felipe Carrillo Puerto.

Columbina talpacoti rufipennis (Bonaparte): Ruddy Ground Dove.—This dove was common at all localities visited. All specimens were in breeding condition.

Specimens (9): ♀, 40472, ova to 3 mm., 45.4 gm. (July 8), ♀, 40468, testis 10 x 5 mm., 50.0 gm (July 8), ♂, 40469, testis 10 x 5 mm., 65.5 gm. (July 8), ♀, 40470, ova to 3 mm., 51.6 gm. (July 8) and ♂, 40471, testis 9 x 5 mm., 57.5 gm. (July 8), all from the vicinity of Puerto Real Isla del Carmen; ♀, 40467, 57.7 gm., (July 10), 5 km. S Chapotón; ♂, 40473, testis 8 x 5 mm., 53.0 gm. (July 17), 1 km. N, 13 km. W Escárcega; ♀, 40465, ova to 21 mm., 51.8 gm. (July 28); Pueblo Nuevo X-can; ♂, 40466, testis 8 x 4 mm., 46.6 gm. (August 16), 4 km. NNE Felipe Carrillo Puerto.

Claravis pretiosa (Ferrari-Perez): Blue Ground Dove.—This species was seen only at Pueblo Nuevo X-can where a breeding pair was taken on July 29; this record extends the known breeding season by one month (see Paynter, 1955b).

Specimens (2): ♂, 40475, testis 10 x 5 mm., 65.0 gm. (July 29), and ♀, 40474, ova to 9 mm., 68.3 gm. (July 29), Pueblo Nuevo X-can.

Leptotila verreauxi fulviventris Lawrence: White-fronted Dove.—My only records of this species are the two specimens listed below. Both birds had slightly enlarged ovaries and the one from west of Escárcega was molting. Paynter (1955a) recorded breeding from late January to late April.

Specimens (2): ♀, 40476, ova to 2 mm., molting—5th and 6th primaries ensheathed (July 14), 7½ km. W Escárcega; ♀, 40477, ovary 12 x 5 mm., 162 gm. (August 14), 4 km. NNE Felipe Carrillo Puerto.

Leptotila jamaicencis gaumeri (Lawrence): Caribbean Dove.—Two were collected on Isla Cozumel and the several white-fronted doves seen on Isla Mujeres probably were of this species.

Specimens (2): ♂, 40478, testis 9 x 5 mm., 175 gm., molting—4th primaries ensheathed (August 9), and ♀, 40479, imm., 116.7 gm., molting—2nd primaries ensheathed (August 10), 3½ km. N San Miguel.

Oreopeleia montana montana (Linnaeus): Ruddy Quail-dove.—My only record is of a male, in full breeding condition, which extends the known breeding period almost two months.

Specimen (1): ♂, 40480, testis 19 x 8 mm., 144.7 gm. (July 29), Pueblo Nuevo X-can.

Artinga astec astec (Souancé): Aztec Parakeet.—This species was most common in deciduous forest and scrub at Champotón, Pisté, Puerto Juarez, and especially Felipe Carrillo Puerto. Parakeets were extremely wary and only two were collected.

Specimens (2): ♂, 40481, testis 3 x 2 mm., 75.0 gm., molting—extensive body molt, 8th primaries ensheathed, middle pair of rectrices are new (August 16), and ♀, 40482, ovary inactive, 72.4 gm. (August 16), 4 km. NNE Felipe Carrillo Puerto.

Amazona xantholora (Gray): Yellow-lored Parrot.—The species was abundant in the vicinity of Champotón. Large flocks congregated near camp; the birds began to assemble about an hour before dark. One was shot from a flock that flew over our camp and another was taken at night from its roost in a small tree about 10 feet above a trail. One small flock of *Amazona* was seen 4 km. NNE Felipe Carrillo Puerto. All specimens were molting.

Specimens (3): ♂, 40483, testis 5 x 2 mm., 229.1 gm., molting—extensive body molt, 6th primaries ensheathed (July 9), and ♀, 40484, ovary 13 x 9 mm. (inactive), 209.0 gm., molting—extensive body molt, wing molt complete (July 11), 5 km. S Champotón; ♂, 40485, testis 5 x 2 mm., 210.9 gm., molting —extensive body molt, 7th primaries ensheathed (August 16), 4 km. NNE Felipe Carrillo Puerto.

Amazona albifrons nana Miller: White-fronted Parrot.—This species was common west of Escárcega where large flocks were seen every evening. A specimen of *A. albifrons* was taken south of Champotón where this species occurred in large flocks with *A. xantholora*. One specimen was taken from a small flock near Chichén-Itzá.

Specimens (5): ♂, 40487, testis 8 x 4 mm., 210.0 gm. (July 10), 5 km. S. Champotón; ♀, 40488, ovary inactive, 205.5 gm., molting (July 12), ♂, 40489, 232.5 gm., molting (July 13), and ♀, 40490, ovary inactive, 206.1 gm. (July 14), 7½ km. W Escárcega; ♀, 40486, ovary inactive, 176.0 gm. (July 27), 2 km. E Chichén-Itzá.

Coccyzus americanus americanus (Linnaeus): Yellow-billed Cuckoo.—A female taken at Pisté substantiates Paynter's (1955a) suggestion that the species breeds on the peninsula.

Specimen (1): ♀, 40491, ovary 12 x 9 mm., 58.7 gm., well-developed brood patch (July 22), Pisté.

Coccyzus minor (Gmelin): Mangrove Cuckoo.—In view of the paucity of recent records of this species from the mainland of the peninsula, it is noteworthy that several individuals were seen flying to and from the beach and mangroves late one evening about 4 km. W Sisal.

Piaya cayana thermophila Sclater: Squirrel Cuckoo.—This species was seen at our camps near Champotón, Pisté, Pueblo Nuevo X-can, and Puerto Juarez. The slightly enlarged (probably regressing) testes of males examined seem to be the only evidence of breeding activity in the species on the peninsula.

Specimens (3): ♂, 40493, testis 8 x 6 mm., 99.6 gm. (July 14), and ♀, 40494, 90.0 gm. (July 14), 7½ km. W Escárcega; ♂, 40492, testis 5 x 2 mm., 97.5 gm., molting (August 14), 4 km. NNE Felipe Carrillo Puerto.

Crotophaga sulcirostris sulcirostris Swainson: Grove-billed Ani.—Three half-grown juveniles were taken at Pisté and a pair in breeding condition was taken at Pueblo Nuevo X-can. These seem to be the first breeding records from the peninsula.

Specimens (5): ♂, 40495, juv., 39.9 gm. (July 21), ♂, 40496, juv., 39.5 gm. (July 21), and ♀, 40497, juv., 30.0 gm. (July 21), Pisté; ♂, 40498, testis 11 x 4 mm., 72.2 gm. (July 28), and ♀, 40499, ova to 7 mm., 70.0 gm. (July 28), Pueblo Nuevo X-can.

Crotophaga ani Linnaeus: Smooth-billed Ani.—The female taken on Isla Cozumel had a slightly enlarged ovary and had been banded (USFWS band no. 524-96303) on the island in 1961 as an adult.

Specimen (1): ♀, 40500, ovary 11 x 7 mm., 86 gm., molting (August 4), 3½ km. N San Miguel.

Glaucidium brasilianum ridgwayi Sharpe: Streaked Pygmy Owl.—A female (40501) was taken by a local boy at Pueblo Neuvo X-can on July 29 weighed 62 gm. and the ovary (7 x 3 mm.) was inactive.

Ciccaba virgata centralis Griscom: Squamulated Owl.—Our only specimen, a female (40502) weighing 288.7 gm. and having an inactive ovary (13 x 4 mm.), was taken at night on July 16 from a mist net stretched across a small trail 1 km. N, 13 km. W Escárcega.

Nyctibius griseus mexicanus Nelson: Mexican Potoo.—One specimen was taken at night 7½ km. W Escárcega where it was found sitting on the limb of a large dead tree. A light but steady rain was falling at the time. On the night of August 16 along a stretch of newly-constructed road 4-16 km. NNE Felipe Carrillo Puerto, 27 potoos were seen, their large and brilliant, amber-colored eyes first appearing in the headlights several hundred yards ahead of our vehicle. All of the birds were perched between 30 and 60 feet above the ground on dead limbs of large trees, and all were perched on the same side of the road facing the light of a full moon. None was less than 200 meters from the next; few flew at the approach of our vehicle. In addition to one specimen taken along the road, another was taken from a fence post in a *milpa* on the same night. It was approached close enough to be shot with a 22 caliber pistol loaded with dust-shot. All specimens had thick layers of subcutaneous and visceral fat and their gonads were small and seemingly inactive.

Specimens (3): sex? 40505 (July 13) 7½ km. W Escárcega; ♀, 40504, ovary 13 x 4 mm. (inactive), 265 gm. (August 16), and ♂, 40503, testis 5 x 3 mm., 320.5 gm. (August 16) 4 km. NNE Felipe Carrillo Puerto.

Chordeiles acutipennis micromeris Oberholser: Trilling Nighthawk.—This species was common in the arid coastal scrub west of Sisal, where hundreds could be seen flying every evening. They were common also at Puerto Juarez, but uncommon at Felipe Carrillo Puerto.

Specimens (2): ♂, 40506, testis 5 x 3 mm., 57.3 gm. (August 1), 5 km. WSW Puerto Juarez; ♀, 40507, ovary 4 x 3 mm. (inactive), 37.0 gm. (August 16), km. NNE Felipe Carrillo Puerto.

Nyctidromus albicollis yucatanensis Nelson: Parauque.—This species was especially common in the vicinity of Felipe Carrillo Puerto and on Isla Cozumel, and was seen at every collecting locality. A flightless, juvenal female was obtained by local boys at Pisté on July 21. Therefore the reproduction period seems to be longer than Paynter's (1955a:141) data suggested.

Specimens (5): ♂, 40512, testis 7 x 3 mm., 75 gm. (July 10), 5 km. S Champotón; ♀, 40508, juv. (remiges and rectrices ensheathed basally), 44.2 gm. (July 21), Pisté; sex? 40510, 55.5 gm. (August 8), and ♂, 40509, testis 3 x 1 mm., 73.5 gm., molting—outermost two pairs of primaries ensheathed (August 10); 3½ km. N San Miguel, Isla Cozumel; ♂, 40511, 72.9 gm. (August 15), 4 km. NNE Felipe Carrillo Puerto.

Caprimulgus salvini badius (Bangs and Peck): Salvin's Whip-poor-will.—My only record of this species is provided by a female (40513) taken 3½ km. N San Miguel, Isla Cozumel, on August 8. The specimen weighed 58 grams, had an inactive ovary (6 x 4 mm.), and was molting (8th and 9th primaries ensheathed).

Chaetura vauxi gaumeri Lawrence: Vaux Swift.—This species was seen at almost every locality visited. The only specimens obtained were brought in by a boy at Pueblo Nuevo X-can on July 30; he said he captured them in his house. Two of them were adults and four were fully-feathered young-of-the-year.

Specimens (6): ♂, 40516, testis 4 x 2 mm., ♀, 40519, ovary inactive, ♂, 40514, juv., 12.6 gm., ♂, 40515, juv., ♀, 40517, juv., and ♀, 40518, juv. (July 30) Pueblo Nuevo X-can.

Campylopterus curvipennis pampa (Lesson): Saber-wing.—A female (40522), shot 7½ km. W Escárcega on July 16, seems to provide the first record of breeding (ovum 6 mm. in oviduct) by this species on the peninsula. A non-breeding female (40521) that weighed 5.0 gms. was taken 4 km. NNE Felipe Carrillo Puerto on August 14.

Chlorostilbon canivetii canivetii (Lesson): Canivet Emerald.—This bird was seen at all localities at which we collected on the mainland.

Specimens (4): ♀, 40530, ovary moderately active, 3.0 gm. (July 22), ♂, 40525, 2.1 gm. (July 23), and sex? 40526, 2.9 gm. (July 25), Pisté; ♀, 40529, ovary inactive, 2.4 gm. (July 26), 3½ km. N Pisté.

Chlorostilbon canivetii forificatus Ridgway: Canivet Emerald.—The specimen is slightly larger than those taken on the mainland and is clearly referable to *C. c. forificatus,* a subspecies endemic to Isla Cozumel.

Specimen (1): ♀, 40534, ovary inactive, 2.8 gm. (August 8), 3½ km. N San Miguel, Isla Cozumel.

Amazilia candida candida (Bourcier and Mulsant): White-bellied Emerald.—This species seemed to be the commonest hummingbird at most localities on the mainland. However, it was not seen along the coasts.

Specimens (5): ♂, 40535, testis 3 mm., 2.9 gm. (July 12), and ♂, 40536, testis 2 mm., 3.6 gm. (July 14), 7½ km. W Escárcega; ♂, 40531, testis 2 mm., 4.3 gm. (July 28), ♂, 40532, 3.8 gm. (July 28), and ♀, 40533, ovary inactive, 3.9 gm. (July 29), Pueblo Nuevo X-can.

Amazilia rutila (DeLattre): Cinnamomeous Hummingbird.—In addition to the two localities from which specimens were taken, several individuals were seen near the airstrip at Puerto Juarez.

Specimens (2): ♀, 40538, ovary inactive, 4.1 gm. (July 30), 1½ km. S, 1 km. E Pueblo Nuevo X-can; ♂, 40539, testis 2 mm. (August 14), 4 km. NNE Felipe Carrillo Puerto.

Amazilia yucatanensis (Cabot): Yucatán Hummingbird.—Many of these hummingbirds were seen among the coco palms on Isla del Carmen. A female taken on August 14 with a moderately enlarged ovary may indicate that the breeding season extends well into the summer.

Specimens (4): ♂, 40540, testis 2 mm., 4.7 gm. (July 7), ♀, 40541, ovary inactive, 3.0 gm. (July 8), and ♂, 40543, 3.0 gm. (July 8); 1 km. SW Puerto Real, Isla del Carmen; ♀, 40542, ovary 6 x 2 mm. (ova to 1 mm.), 2.9 gm. (August 14), 4 km. NNE Felipe Carrillo Puerto.

Trogon citreolus melanocephala Gould: Citreoline Trogon.—This species was heard or seen at all localities where deciduous forest was present.

Specimens (7): ♀, 40557, ovary 14 x 8 mm. (ova to 2 mm.), brood patch, 72.5 gm. (July 16), and ♂, 40558, 66.5 gm. (July 16), 7½ km. W Escárcega; ♂, 40553, 74.0 gm. (August 1), ♀, 40552, 74 gm. (August 1), ♀, 40554, ova to 3 mm. (August 2), and ♂, 40555, 76.2 gm. (August 2), 4 km. WSW Puerto Juarez; ♀, 40556, 76.4 gm. (August 15), 4 km. NNE Felipe Carrillo Puerto.

Chloroceryle americana septentrionalis (Sharpe): Green Kingfisher.—My only specimen is a male (40559) shot near a large aguada at Rancho San Miguel, 4 km. NNE Felipe Carrillo Puerto on August 16. The specimen weighed 40.5 gm.

Ceryle torquata (Linnaeus): Ringed Kingfisher.—Paynter (1955a:154) noted that this "species has not been recorded from Yucatán but it is undoubtedly present, at least in the sheltered lagoon behind the barrier bar." A single individual was seen in one of these lagoons on August 9 and 10.

Eumomota superciliosa superciliosa (Sandbach): Turquoise-browed Motmot.—On July 9 this species was nesting in a large "colony" 5 km. S Champotón, Campéche, in a large abandoned gravel pit having vertical banks about 10 feet high. The pit was an irregular semicircle with an approximate radius of 100 yards and was bordered by a road on one side and elsewhere by low scrub vegetation. The pit was one of several found in the area and formerly was used as a source of limestone gravel used in constructing the road between Champotón and Escárcega. The exposed limestone substratum was overlaid with chalky soil six to eight feet deep.

Motmots were nesting in burrows dug in the layer of surface soil. A total of 101 burrows seemed to be in use or to have been used in 1962. Nine appeared to be unused and 24 burrows evidently were abandoned before they were finished. The depths of 12 burrows selected at random were 34, 32, 37, 25, 28, 44, 36, 36, 24, 37, 22, and 43 inches, and averaged 33.4 inches. In cross-section the burrows varied from round (three inches in diameter) to oval (three inches high and four inches wide). The inner ends of the burrows were enlarged with a depression in the floor, where the eggs were laid.

The long axes of most burrows were straight and perpendicular to the face of the bank in which they were dug; two burrows nevertheless were curved laterally, and one was U-sharped, having two entrances that opened about 12 inches apart.

Eggs and nestlings were found lying on the bare soil at the inner ends of the burrows; no nesting material was found.

The contents of 10 burrows that were excavated are summarized in Table 1.

TABLE 1. Contents of 10 burrows of Turquoise-browed Motmots.

Burrow	Fresh	Eggs	Nestlings	Post-fledgling
1	°			
2		4		
3		3		
4		4		
5		1	3	
6			4	
7			1	
8		x		
9				°
10				°

° Nothing.
x Broken egg shells.

Three nests contained no eggs or young. One of these was freshly dug. The other two empty burrows apparently had been recently occupied by nestlings and contained the foul smelling remains of fecal material, hundreds of beetle wings, and other undigestible parts of insects. The manure was teeming with large fly larvae.

Three burrows contained nestlings; one had four young with pin feathers, one a chick fully feathered, and one three newly hatched young and one egg.

In burrow 2, three eggs had advanced embryos and one was infertile; in burrow 3, the eggs had small embryos; and in burrow 4, the eggs appeared fresh. Burrows 3 and 4 were occupied by adult birds that did not flush during the excavation of their burrows. They were easily caught by hand and later prepared as specimens. One was a male and the other a female; each had a brood patch.

Possibly females of this species raise more than one brood in a single nesting season, but I have no direct evidence of this. Such an hypothesis is suggested by the different stages of nestings found in the burrows. Moreover, there were more than twice as many burrows as motmots in the area. The largest number of individuals counted at any time near the colony was 20 adults (about an hour after sunrise). Assuming that all of these birds had mates, the maximum number of adults present could have numbered about 40.

There is another bit of evidence for double broods. Because of fouling of the burrow that accompanies the raising of a brood of young, it seems improbable that a burrow would be used immediately for a second nesting attempt. Consequently digging a second burrow would be necessary, if a second brood is raised.

Most of my observations are in keeping with Skutch's detailed report (1947) of the species in Central America. According to him, eggs are laid in April and May in Honduras and Guatamala, although he did not state that breeding does not occur in other months. The observations in Campeche in early July suggest that breeding can occur over an extended period; Paynter (1955a:158) found the species to be in various stages of reproductive activity in April on the peninsula.

Skutch suggested that the motmots he observed in Central America were solitary nesters, and nest in "groups" only where suitable nesting sites are scarce. In Campeche, many suitable, seemingly identical, but unused, nesting sites were available within a few hundred yards of the site of the actual nesting

"colony." Moreover, most of the burrows were only a few feet apart and no agonistic behavior was witnessed. It seems that this motmot is characterized by colonial nesting habits in Campeche, even where abundant sites for individual nesting efforts are available.

The species was abundant around the *cenotes* at Chichén-Itzá; adults with enlarged gonads and brood patches and juveniles were taken at Pisté as late as July 21.

Specimens (19): ♂, 40565, brood patch, 59.4 gm. (July 9), ♂, 40564, testis 8 x 4 mm., brood patch, 68.0 gm. (July 9), ♂, 40566, 74 gm. (July 9), ♀, 40567, juv. (July 9), ♂, 40568, testis 5 x 3 mm., 68.3 gm. (July 10), ♂, 40578, 59.5 gm. (July 11), and ♀, 40577, ova to 2 mm., brood patch, 65.2 gm. (July 11), all from 5 km. S Champotón; ♂, 40560, 43.6 gm. (July 20), ♀, 40562, brood patch, 55 gm. (July 21), sex? 40561, 64 gm. (July 21), and ♀, 40563, juv. (July 22), Pisté. Eight nestlings (40569-76) that were taken from burrows at 5 km. S Champotón on July 11 had the following weights: 42.4 gm., 39.7 gm., 38.5 gm., 12.2 gm., 40.0 gm., 30.7 gm., 26.8 gm., 19.0 gm. Mallophaga: *Philopterus* sp., July 9.

Momotus momota lessonii Lesson: Blue-crowned Motmot.—For convenience, the specimens from 5 km. S Champotón are assigned to *M. m. lessonii* on the basis of measurements (wing 139 mm., tail 240 mm., culmen [from feathers] 41.0 mm.) taken on one specimen (40579), which are within the limits of the subspecies as described by Ridgway (1914). Two other specimens from that locality were prepared as skeletons and their weights are essentially the same as those Paynter (1955a) recorded for *M. m. lessonii*. According to Paynter, there is a southward clinal increase in size in this species between the smaller *M. m. exiguus* in the northern part of the peninsula and *M. m. lessonii* in the extreme southern part. A more extensive series of specimens from the vicinity of Champotón probably would reveal a population intermediate in size between the typical representatives of the two races.

Specimens (3): ♀, 40579, 105 gm. (July 10), ♀, 40581, 98.9 gm. (July 11), ♂, 40580, 102.5 gm. (July 11), 5 km. S Champotón.

Pteroglossus torquatus erythrozonus Ridgway: Collared Aracari.—A male taken at Pueblo Nuevo X-can on July 27 and a female from 4 km. NNE Felipe Carrillo Puerto on August 15 had slightly enlarged gonads, which probably were regressing. Apparently these are the first indications of breeding activity for this species on the peninsula.

Specimens (5): ♂, 40586, testis 4 x 2 mm., 155 gm. (July 16), 7½ km. W Escárcega; ♂, 40582, testis 10 x 5 mm., 169.1 gm. (July 27), and ♀, 40583, ovary inactive, 137.3 gm. (July 29), Pueblo Nuevo X-can; ♀, 40584, ovary 10 x 6 mm., 169.5 gm. (August 15), and sex? 40585, 148.9 gm. (August 16), 4 km. NNE Felipe Carrillo Puerto.

Rhamphastos sulfuratus sulfuratus Lesson: Keel-billed Toucan.—This species was especially common west of Escárcega, where it was most often seen in small flocks of less than 10 birds. Presumably breeding had already occurred; four specimens had inactive gonads.

Specimens (7): ♀, 40589, 367.3 gm. (July 12), ♂, 40588, testis 8 x 3 mm., 414.5 gm. (July 14), ♀, 40590, ovary 11 mm., 347.4 gm. (July 15), ♂, 40591, testis 5 x 3 mm., 371 gm. (July 15), ♂, 40593, testis 6 x 3 mm., 422.2 gm. (July 16) and ♂, 40592, 401.5 gm. (July 16), 6-7½ km. W Escárcega; ♀, 40587, 395.5 gm. (July 28), Pueblo Nuevo X-can.

Piculus rubiginosus yucatanensis (Cabot): Red-capped Green Woodpecker. —Specimen (1): ♀, 40594, ovary inactive (7 x 4 mm.), extensive body molt, 67.7 gm. (August 17), 4 km. NNE Felipe Carrillo Puerto. Mallophaga: *Penerirmus* sp.

Drycopus lineatus similis (Lesson): Lineated Woodpecker.—Specimen (1): ♂, 40595, molting, 141.2 gm. (July 15), 7½ km. W Escárcega.

Centurus aurifrons dubius (Cabot): Golden-fronted Woodpecker.—The gonads were moderately enlarged in several of the specimens taken in the first half of July. The plumage was much worn in all specimens and some were in early stages of molt. Apparently the breeding season on the peninsula extends to at least mid-July. The specimen from Isla Cozumel is assigned to *C. a. dubius,* following the systematic treatment by Selander and Giller (1963).

Specimens (10): sex? 40602, 75.0 gm. (July 8), and ♀, 40601, ovary 6 x 3 mm. (enlarged oviduct), 76.4 gm. (July 10), 1 km. S Puerto Real, Isla del Carmen; ♂, 40599, testis 6 x 8 mm., 101.3 gm. (July 10), and ♂, 40600, 86.0 gm. (July 11), 5 km. S Champotón; ♂, 40603, testis 5 x 3 mm. (July 14), and ♀, 40604, ovary 6 x 4 mm. (ova to 1 mm.), brood patch (July 16), 7½ km. W Escárcega; sex? 40596, molting, much visceral fat, 79.0 gm. (July 22), Pisté; ♀, 40597, 73.7 gm. (July 28), Pueblo Nuevo X-can; ♀, 40598, 79.6 gm. (August 15), 4 km. NNE Felipe Carrillo Puerto; ♂, 40605, testis inactive, molting, much visceral fat (August 8), 3.5 km. N San Miguel, Isla Cozumel.

Centurus pygmaeus (Peters): Yucatán Woodpecker.—Paynter (1955a: 166) reported evidence of breeding in this species on April 3 and May 23; a male having enlarged testes was taken on July 10.

Specimens (5): ♂, 40608, testis 6 x 4 mm. (July 10); ♀, 40607, 39.5 gm. (July 10), 5 km. S Champotón; ♂, 40609, testis inactive, 35.8 gm., moderate visceral fat (July 17), 1 km. N, 13 km. W Escárcega; ♀, 40606, ovary 6 x 4 mm. (inactive), 37.0 gm. (August 14), 4 km. NNE Felipe Carrillo Puerto; ♂, 40610, testis inactive, heavy visceral and subcutaneous fat, 41.6 gm., (August 10), 3½ km. N San Miguel, Isla Cozumel.

Phloeoceastes guatemalensis guatemalensis (Hartlaub): Guatemalan Ivory-billed Woodpecker.—Specimens (4): ♂, 40611, right testis 2 mm., left testis vestigial, 203.7 gm. (July 23), Pisté; 40612, sex? 212 gm., (July 28), and ♀, 40613, 218.1 gm. (July 30), Pueblo Nuevo X-can; ♀, 40614, 189.2 gm. (August 15), 4 km. NNE Felipe Carrillo Puerto.

Dendrocincla anabatina Sclater: Tawny-winged Woodhewer.—Specimen (1): ♂, 40615, testis 2 x 1 mm., 35.7 gm., molting—5th primaries and middle pair of rectrices ensheathed (July 17), 1 km. N, 13 km. W Escárcega.

Dendrocincla homochroa homochroa (Sclater): Ruddy Woodhewer.—May 20 seems to be the only previous date of record for breeding in this species (Paynter, 1955a:171); our specimen extends the known season nearly three months.

Specimen (1): ♀, 40616, ovary 13 x 6 mm. (ova to 2 mm.), brood patch, 35.1 gm. (August 16), 4 km. NNE Felipe Carrillo Puerto.

Sittasomus griseicapillus (Vieillot): Olivaceous Woodcreeper.—Specimens (2): ♂, 40617, juv., 11.2 gm. (July 26), Pisté; ♀, 40618, ovary inactive, 10.5 gm. (August 15), 4 km. NNE Felipe Carrillo Puerto.

Xiphorhynchus flavigaster (Swainson): Ivory-billed Woodcreeper.—According to Paynter (1955a:173), indications of breeding have been observed in specimens of this species taken between March 27 and June 5. A male taken on August 15 had moderately enlarged (probably regressing) testes and was well into the molt.

Specimen (1): ♂, 40619, testis 5 x 3 mm., 51.5 gm., molting—5th primaries and middle pair of rectrices ensheathed (August 15), 4 km. NNE Felipe Carrillo Puerto.

Lepidocolaptes souleyetii (Des Murs): Streak-headed Woodhewer.—This appears to be the second specimen recorded from the peninsula (see Traylor, 1941).

Specimen (1): ♂, 40621, testis 3 x 1 mm., 26.6 gm., molting—6th primaries ensheathed, middle pair of rectrices are new (July 17), 1 km. N, 13 km. W Escárcega.

Synallaxis erythrothorax Sclater: Rufous-breasted Spinetail.—Specimen (1): ♂, 40622, imm. skull, 16.1 gm. (August 16), 4 km. NNE Felipe Carrillo Puerto.

Thamnophilus doliatus (Linnaeus): Barred Antshrike.—Specimen (1): ♀, 40623, ovary 8 x 5 mm. (inactive), 26 gm. (August 14), 4 km. NNE Felipe Carrillo Puerto.

Formicarius analis (d'Orbigny and Lafresnaye): Black-chinned Antthrush.—Specimen (1): ♂, 40624, 56.0 gm. (July 29), Pueblo Nuevo X-can.

Pachyramphus major itzensis Nelson: Mexican Becard.—Previous records of breeding in this species are provided by a female obtained on July 12 (Paynter, 1955a:182) and a male taken on June 9 (Paynter, 1955b).

Specimen (1): ♂, 40625, testis 9 x 5 mm., 22.1 gm. (July 21), Pisté.

Platypsaris aglaiae (Lafresnaye): Rose-throated Becard.—All specimens have extensively worn plumage.

Specimens (3): ♂, 40628, 33.5 gm. (July 10), 5 km. S Champotón; ♀, 40626, ovary 6 x 3 mm., brood patch, 34.0 gm. (July 20), ♀, 40627, ovary inactive, 33.9 gm. (July 26); 3½ km. N and 6½ km. W Pisté.

Tityra semifasciata personata Jardine and Selby: Masked Tityra.—Previously, breeding information for this species has been available only for March (Paynter, 1955a:184). Adults were observed feeding young fledglings 7½ km. W Escárcega on July 15, and a juvenile was taken. Gonads of males were in full breeding condition.

Specimens (5): ♂, 40630, testis 13 x 6 mm., 81.3 gm. (July 14), sex? 40631, juv., 55.5 gm. (July 15), ♂, 40632, testis 9 x 5 mm., 73 gm., molting—1st and 2nd primaries ensheathed (July 15), and ♀, 40633, 84.7 gm. (July 16), 7½ km. W Escárcega; ♀, 40629, ova to 1 mm., 80.0 gm. (July 23), Pisté.

Erator inquisitor fraserii (Kaup): Black-capped Tityra.—Breeding has been recorded by Paynter (1955a:185) on April 26. A moderately enlarged testis (probably regressing) was noted in the specimen from Pisté, on July 21.

Specimens (2): ♂, 40635, 51.8 gm. (July 15), 7½ km. W Escárcega; ♂, 40634, testis 6 mm., 51 gm., molting—6th primaries ensheathed (July 21), Pisté.

Pipra mentalis mentalis Sclater: Red-capped Manakin.—The specimens here reported seem to be the first from the peninsula in which reproductive activity has been recorded.

Specimens (2): ♂, 40637, testis 5 x 3 mm., 14.0 gm. (July 29), Pueblo Nuevo X-can; ♂, 40636, testis 5 x 2 mm., 14.6 gm. (August 3), 4 km. WSW Puerto Juarez.

Pyrocephalus rubinus (Boddaert): Vermillion Flycatcher.—This species was seen only in the arid scrub 2-13 km. WSW of Sisal. Breeding seemingly had ended by early August, as evidenced by four adults that showed no gonadal activity and were in advanced stages of molt.

Specimens (5): ♀, 40638, juv., 12.1 gm. (August 7), 1½ mi. S Sisal; ♀, 40640, ovary inactive, 14.1 gm., molting—6th primaries ensheathed (August 10), ♀, 40641, ovary inactive, 13.9 gm., molting—7th primaries ensheathed (August 10), and ♂, 40642, testis 2 mm., 14.6 gm., molting—5th primaries ensheathed (August 10), 13 km. WSW Sisal; ♀, 40639, testis 1 mm., 14.0 gm., molting—7th primaries ensheathed (August 18), 2 km. SW Sisal.

Tyrannus melancholicus chloronotus Berlepsch: Tropical Kingbird.—Most specimens were molting. A male and two females from Pisté taken on July 21 and a female from Pueblo Nuevo X-can (July 29) had slightly enlarged (probably regressing) gonads. Three immatures were collected and adults were seen feeding young fledglings at Pisté. There seems to be no other breeding records from the peninsula.

Specimens (10): ♀, 40650, 42 gm., (July 10), 5 km. S Champotón; ♀, 40752, ovary inactive, 43.4 gm., molting—4th primaries ensheathed (July 14), and ♂, 40651, imm., 42.5 gm. (July 15), 6-7½ km. W Escárcega; ♀, 40645, ovary slightly enlarged (8 x 3 mm.), 47.5 gm. (July 21), ♀, 40643, ova to 1 mm., 39.3 gm. (July 21), ♂, 40644, testis 10 x 7 mm., 43.1 gm., starting to molt—1st primaries ensheathed (July 21), and ♀, 40646, imm., (July 26), Pisté; ♀, 40648, ova to 1 mm., 37.4 gm. (July 29), Pueblo Nuevo X-can; ♂, 40647, imm., 38.4 gm. (August 14), and ♀, 40649, 44.4 gm., molting—only outer 3 pairs of rectrices present and are ensheathed basally, 6th and 7th primaries ensheathed (August 15), 4 km. NNE Felipe Carrillo Puerto.

Myiodynastes luteiventris luteiventris Sclater: Sulfur-bellied Flycatcher.—The latest breeding record given by Paynter (1955a:191) is for the last week in June. A male taken on July 31 had enlarged testes. None of the following specimens was in the process of molt.

Specimens (4): ♀, 40655, 44.5 gm. (July 10), 5 km. S Champotón; ♀, 40656, ovary slightly enlarged (8 x 4 mm.), 47.0 gm. (July 15), 7½ km. W Escárcega; ♀, 40654, testis 10 x 4 mm., 39 gm. (July 31), Pueblo Nuevo X-can.

Megarhynchus pitangua mexicanus (Lafresnaye): Boat-billed Flycatcher.—I know of no previous breeding record for this species on the peninsula. The female obtained on July 25 was observed feeding young.

Specimens (2): ♀, 40658, 57.6 gm. (July 11), 5 km. S Champotón; ♀, 40657, ovary 10 x 5 mm., 59.8 gm. (July 25), Cenote Seco, 2 km. E Chichén-Itzá.

Myiozetetes similis texensis (Giraud): Vermilion-crowned Flycatcher.—Paynter (1955a:192) reported this species breeding in mid-May. A male taken on July 17 west of Escárcega had enlarged (probably regressing) testes and indicates breeding later than May.

Specimens (3): ♂, 40660, testis 6 x 3 mm., 32.0 gm. (July 17), and sex? 40661, 33.8 gm., molting—5th primaries ensheathed (July 17), 1 km. N, 13 km. W Escárcega; ♂, 40659, imm., testis 2 x 1 mm., 27.6 gm. (July 29), Pueblo Nuevo X-can.

Pitangus sulphuratus guatimalensis (Lafresnaye): Great Kiskadee.—Apparently our specimens, which were in the late stages of breeding, are the first evidence of reproduction for the species on the peninsula.

Specimens (4): ♀, 40663, ova to 1 mm., 50.7 gm. (July 9), and ♂, 40664, right testis 12 mm., 65.0 gm., body feathers in early stages of molt (July 9), 5 km. S Champotón; ♂, 40665, testis 5 mm., 61.9 gm., molting—middle pair of rectrices are new, 6th primaries ensheathed (July 15), 7½ km. W Escárcega; sex? 40662, 59.5 gm. (August 14), 4 km. NNE Felipe Carrillo Puerto. Mallophaga: *Philopterus* sp.

Myiarchus tyrannulus cooperi Baird: Wied Flycatcher.—This species was especially common among the coco palms on Isla del Carmen and Isla Cozumel.

Specimens (5): ♂, 40667, 36.7 gm. (July 8), ♂, 40668, 36.6 gm. (July 8), sex? 40669, 39.4 gm. (July 8), and ♀, 40670, 37.3 gm. (July 8), all from 1 km. SW Puerto Real, Isla del Carmen; ♀, 40666, ovary inactive, 34.9 gm. (August 10), 3 km. N San Miguel, Isla Cozumel.

Myiarchus tuberculifer platyrhynchus Ridgway: Olivaceous Flycatcher.—Breeding specimens of this species have been known previously from April and May (Paynter, 1955a:196); records listed beyond extend the season nearly three months.

Specimens (7): ♀, 40673, ova to 5 mm. (July 10), and ♀, 40674, ovary 7 x 3 mm. (ova to 1 mm.) (July 11), 5 km. SW Champotón; ♀, 40745, ovary inactive, 17.5 gm., starting to molt—1st, 2nd, and 3rd primaries ensheathed (July 16), 7½ km. W Escárcega; ♀, 40671, imm., 16.1 gm. (July 20) Cenote Seco, 2 km. E Chichén-Itzá; ♂, 40746, 18.2 gm. (July 22), Pisté; ♀, 40672, ovary inactive, 17.7 gm., molting—5th and 6th primaries and 1st secondaries ensheathed (August 15), 4 km. NNE Felipe Carrillo Puerto; ♂, 40675, left testis 13 mm., right testis 10 mm., 17.5 gm. (August 8), 3½ km. N San Miguel, Isla Cozumel.

Contopus cinereus (Spix): Tropical Pewee.—The regressing gonads of the male taken on July 21 in an early stage of molt suggests breeding on the peninsula.

Specimens (2): ♂, 40676, testis 6 x 3 mm., 11.5 gm., starting to molt—1st and 2nd primaries ensheathed (July 21), 6½ km. W Pisté; ♂, 40677, testis 1 mm., 12.6 mm., molting—4th, 5th, and 6th primaries and 2nd secondaries ensheathed (August 14), 4 km. NNE Felipe Carrillo Puerto.

Tolmomyias sulphurescens (Spix): Sulphury Flat-Billed Flycatcher.—Paynter (1955a:201) presented breeding records for this species from mid-April to late June. My specimens seem to indicate that breeding extends at least into July.

Specimens (6): ♀, 40683, juv., 14.0 gm. (July 21), ♂, 40684, juv. (remiges and rectrices ensheathed basally), 14.0 gm. (July 21), and ♂, 40682, testis 8 x 4 mm., 13.7 gm. (July 26), Pisté and 3½ km. N Pisté; ♂, 40685, testis 7 x 4 mm., 15.3 gm., molting—1st and 2nd primaries ensheathed (July 28), and ♀, 40686, ovary inactive (July 28), Pueblo Nuevo X-can; ♂, 40687, imm., 16.0 gm. (August 15), 4 km. NNE Felipe Carrillo Puerto. Mallophaga: *Philopterus* sp. July 28; *Myrsidea* sp. July 28.

Myiopagis veridicata (Vieillot): Yellow-crowned Elaenia.—The only previous breeding record is of a male that was taken on April 29. My only specimen has nearly fully enlarged testes.

Specimen (1): ♂, 40688, testis 7 x 4 mm., 13.1 gm. (July 17), 1 km. N, 13 km. W Escárcega.

Progne subis subis (Linnaeus): Purple Martin.—A large migrant flock of several thousand individuals of this species was present for several days in August at Rancho San Miguel.

Specimens (3): ♀, 40723, ovary inactive, 48.6 gm. (August 14), ♀, 40724, 51.8 gm. (August 17), and ♀, 40725, imm. skull, 52.1 gm. (August 17), 4 km. NNE Felipe Carrillo Puerto.

Petrochelidon fulva citata Van Tyne: Cave Swallow.—Throughout our stay at Pisté, large numbers of Cave Swallows were seen flying in and out of the small opening of a well-like *cenote* in the center of the village. Specimens were easily collected in a mist net placed across the opening. No young Cave Swallows were taken and gonads of adults were in various stages of reproductive activity. A few individuals taken were beginning to molt. Probably the swallows were nesting in the *cenote* although the nests were inaccessible to view. Previous breeding records are for April (Paynter, 1955a:209).

Twenty-two specimens were collected, of which the following were taken at Pisté, July 21-25: ♂, 40693, testis 6 x 3 mm., 18.4 gm.; ♂, 40696, 16.4 gm.; ♀, 40697, 18.2 gm.; ♂, 40695, 15.0 gm.; ♀, 40690, ovary inactive, 18.4 gm., molting—2nd primaries ensheathed; ♂, 40692, testis 5 x 3 mm., 17.9 gm.; ♀, 40698, 18.3 gm.; ♀, 40702, ovary 7 x 3 mm., 18.9 gm.; ♀, 40703, ovary 6 x 3 mm., 17.5 gm.; ♂, 40713, testis 3 mm., 18.4 gm.; ♀, 40704, 16.5 gm.; ♂, 40705, 20.3 gm.; ♂, 40699, testis 2 mm., 18.6 gm., molting—2nd primaries ensheathed; ♀, 40700, ovary 5 x 3 mm., 18.5 gm., molting—1st primaries ensheathed; ♀, 40701, ovary 5 x 3 mm., 16.5 gm., molting—1st primaries ensheathed; ♂, 40707, testis 7 x 5 mm., 19.9; ♂, 40708, testis 4 x 3 mm., 18.4 gm.; ♀, 40709, ovary 4 x 3 mm., 18.0 gm.; sex? 40711, 18.3 gm., molting—1st and 2nd primaries ensheathed.

Additional specimens are: ♀, 40718, 16.5 gm., molting—3rd primaries ensheathed (August 16), and ♀, 40719, 18.5 gm., molting 1st primaries ensheathed (August 16), 4 km. NNE Felipe Carrillo Puerto; ♂, 40689, testis 1 mm., 16.2 gm., molting—2nd primaries ensheathed (August 10), 13 km. WSW Sisal. Mallophaga: *Philopterus excisus,* July 21; *Myrsidea* sp. July 21 and 25.

Stelgidopteryx ruficollis Audubon: Rough-winged Swallow.—Previous records indicate that three subspecies of this species occur on the Yucatán Peninsula (Paynter, 1955a:209). One of these, S. *r. ridgwayi,* is resident. S. *r. serripennis,* representing the breeding population occurring from British Columbia and New Hampshire over much of the United States to central California, central Texas, and the Gulf states, has been taken on the peninsula in winter. Paynter referred two specimens taken in late September and three January-taken specimens to S. *r. stuarti,* the highland race that breeds from the mountains of southern Veracruz to Guatamala.

Allan R. Phillips had identified two immature individuals (40694 and 40712) from Pisté as S. *r. stuarti;* one specimen from Puerto Juarez also is an immature and is nearly identical to those from Pisté. Two adults from Pisté (40691 and 40710) are noticeably darker dorsally than the immatures but are molting extensively and their identification to subspecies is equivocal. Two other adults (40706 and 40715) were prepared as skeletons.

Although mid-July seems early for S. *r. stuarti* to be present on the peninsula it is not too surprising since the three specimens positively identified are immature birds and young possibly arrive earlier than do adults. But, the immature specimens possibly are atypical individuals of the resident population of S. *r. ridgwayi.*

Except for the immature individual from 5 km. WSW Puerto Juarez, all specimens were taken in mist nets over the *cenote* at Pisté where *Petrochelidon fulva* also was obtained.

Specimens (7): ♂, 40694, imm., 16.2 gm., ♀, 40691, ovary inactive, 16.4 gm., molting—general body molt, 5th primaries and middle pair of rectrices ensheathed, ♀, 40712, imm., 14.5 gm., ♀, 40706, 14.8 gm., ♂, 40715, 16.4 gm., ♂, 40710, 18.5 gm., molting—general body molt, 1st primaries and middle pair of rectrices ensheathed, all from Pisté, July 21 and 25; ♂, 40720, imm., 15.5 gm. (August 1), 5 km. WSW Puerto Juarez.

Hirundo rustica erythrogaster Boddaert: Barn Swallow.—Specimen (1): ♀, 40721, imm., 7.3 gm. (August 18), apparently an early migrant, 2 km. WSW Sisal.

Iridoprocne albilinea (Lawrence): Mangrove Swallow.—Specimen (1): ♀, 40722, imm. (July 7), Puerto Real, Isla del Carmen.

Cissilopha yucatanica (Dubois): Yucatán Jay.—Heretofore, breeding activity has been recorded only in March (Paynter, 1955a:217). All specimens in my collection have extensively worn plumage and were beginning to molt.

Specimens (6): ♂, 40726, left testis 9 x 7 mm., right testis 4 x 2 mm., brood patch, 122.3 gm., molting—1st and 2nd primaries ensheathed (July 10), 5 km. S Champotón; ♂, 40727, testis 5 x 3 mm., brood patch, 125.6 gm., molting—1st and 2nd primaries ensheathed (July 11), 5 km. SW Champotón; ♀, 40728, 109.8 gm. (July 13), and sex? 40729, 109.5 gm. (July 15), 7½ km. W Escárcega; ♀, 40730, imm., 110.3 gm. (July 21), Pisté; ♀, 40731, ovary inactive, brood patch refeathering, 121 gm., molting—2nd and 3rd primaries ensheathed (August 16), 4 km. NNE Felipe Carrillo Puerto.

Cyanocorax yncas maya (van Rossem): Green Jay.—There are records of breeding by this species on the peninsula for April 28 and 29, and June 4 (Paynter, 1955a:215, 216).

Specimens (4): ♂, 40740, testis 5 x 3 mm., 81.2 gm. (July 16), 7½ km. W Escárcega; ♀, 40739, juv., 62.3 gm. (July 21), ♂, 40737, 64.5 gm. (July 21), and ♀, 40738, 64.1 gm. (July 21), Pisté.

Psilorhinus morio (Wagler): Brown Jay.—Specimens (3): ♀, 40742, 203.5 gm. (July 13), ♂, 40743, juv., 170 gm. (July 14), 7½ km. W Escárcega; ♂, 40741, juv., 193.7 gm. (August 14), 4 km. NNE Felipe Carrillo Puerto.

Thryothorus lucovicianus albinucha (Cabot): Carolina Wren.—This wren formerly was considered to be a species (*T. albinucha*). In the light of evidence presented by Lowery and Berrett (1963), it is advisable to follow Paynter (1955a:219) and consider *albinucha* to be a subspecies of *T. ludovicianus*. The only previous evidence of breeding by this species on the peninsula was a male having slightly enlarged gonads taken by Paynter (1955a: 219) on March 9.

Specimen (1): ♂, 40754, juv., 16.8 gm. (August 14), 4 km. NNE Felipe Carrillo Puerto.

Thryothorus maculipectus canobrunneus Ridgway: Spotted-breasted Wren. —According to Paynter (1955a:220) this species breeds from mid-March to May 23. Gonads were moderately active in our specimens as early as mid-July.

Specimens (4): ♀, 40758, ovary (6 x 3 mm.) granular (July 14), and ♂, 40757, testis 5 x 3 mm., 15.3 gm. (July 14), 7½ km. W Escárcega; ♀, 40755, ovary 6 x 3 mm. (ova to 1 mm.), 12.7 gm. (July 21), Pisté; ♀, 40756, ovary 4 x 3 mm., 16.8 gm. (August 3), 4 km. WSW Puerto Juarez.

Troglodytes musculus Naumann: Southern House Wren.—Specimen (1): ♀, 40760, juv. (August 2), 4 km. WSW Puerto Juarez.

Troglodytes beani Ridgway: Cozumel Wren.—Specimens (2): ♀, 40761, 13.3 gm. (August 9), and ♂, 40762, imm., 13.6 gm. (August 9), 3½ km. N San Miguel, Isla Cozumel.

Campylorhynchus yucatanicus (Hellmayr): Yucatán Wren.—This species was abundant in the coastal scrub west of Sisal where some breeding activity was noted. A few individuals were carrying nest material and several were feeding young. There were many old and abandoned nests and apparently the breeding season was nearly over. The only previous breeding record is for March 19 when a newly completed nest was found (Paynter, 1955a:218).

Specimens (4): ♂, 40750, imm., 32.4 gm. (August 7), 1½ mi. SW Sisal; ♀, 40751, imm., 31.2 gm. (August 18), 2 km. WSW Sisal; ♀, 40752, ovary 7 x 3 mm., 40 gm. (August 9), 4.3 km. WSW Sisal; ♀, 40753, 31.0 gm. (August 11), 6½ km. WSW Sisal.

Melanoptila glabrirostris cozumelana (Paynter): Black Catbird.—Apparently the only previous record of breeding by this species was Paynter's (1955b) mention of a male from Quintana Roo with enlarged gonads on June 26. The three adults in the collection here reported on were in nearly full reproductive activity.

Specimens (4): ♂, 40764, imm., 40.5 gm. (August 8), ♂, 40767, testis 8 x 4 mm., 42.0 gm., heavy fat (August 8), ♀, 40765, ovary active (oviduct enlarged), brood patch, 35.2 gm. (August 10), and ♂, 40766, testis 9 x 6 mm., 35 gm. (August 10), from 2½-3½ km. N San Miguel, Isla Cozumel.

Mimus gilvus (Vieillot): Tropical Mockingbird.—The only breeding record heretofore is by Paynter (1955a:226) of newly-fledged juveniles taken on May 26 and 29. Gonads in our adults were moderately active; feathers were extremely worn, but molting was not evident.

Specimens (4): ♂, 40771, testis 9 x 6 mm., 51.0 gm. (July 9), 5 km. S Champotón; ♀, 40770, ovary moderately active (ova to 2 mm.), brood patch, 42 gm., moderate fat (August 9), 3½ km. N San Miguel, Isla Cozumel; ♀, 40768, imm., 45.2 gm., moderate fat (August 18), 2 km. WSW Sisal; ♂, 40769, testis 10 x 5 mm., 51.8 gm. (August 9), 13 km. WSW Sisal. Mallophaga: *Myrsidea* sp., July 9.

Toxostoma guttatum (Ridgway): Cozumel Thrasher.—Our specimen had enlarged testes and seems to represent the first record of breeding activity in the species.

Specimen (1): ♂, 40772, testis 7 x 4 mm., 49.5 gm. (August 10), 3½ km. N San Miguel, Isla Cozumel.

Turdus grayi Bonaparte: Clay-colored Robin.—Four adults were in full breeding condition.

Specimens (6): ♂, 40780, testis 13 x 8 mm., brood patch (July 10), 5 km. S Champotón; ♀, 40781, ova to 8 mm., 79.6 gm. (July 15), 5 km. SW Escárcega; ♀, 40776, 61.3 gm. (July 21), Pisté; ♀, 40777, imm., 63.4 gm. (July 20), 6½ km. W Pisté; ♂, 40779, testis 14 x 8 mm., brood patch, 68.5 gm. (July 30), and ♂, 40778, testis 13 x 11 mm., 71.5 gm. (July 28), Pueblo Nuevo X-can.

Polioptila caerulea (Linnaeus): Blue-gray Gnatcatcher.—A fledgling taken at Pisté was barely flying with remiges and rectrices ensheathed basally. Previous breeding records are for April 11 and 27 (Paynter, 1955a:231). A male taken on August 10 on Isla Cozumel had nearly completed molting into winter plumage.

Specimens (8): ♀, 40788, fledgling, 5.0 gm. (July 20), 6½ km. W Pisté; ♂, 40787, testis 2 x 1 mm., 5.6 gm. (July 21), ♂, 40785, juv., 5.8 gm. (July 22), and ♀, 40786, 5.6 gm. (July 22), Pisté; ♀, 40791, juv., 5.6 gm. (August 8), ♂, 40790, juv., 5.8 gm. (August 8), ♀, 40789, 5.7 gm. (August 9), and ♂, 40792, 5.3 gm., molting—7th primaries ensheathed (August 10), from 2½-3½ km. N San Miguel, Isla Cozumel.

Polioptila albiloris Lawrence: White-lored Gnatcatcher.—This species was abundant in the arid scrub along the coast in the vicinity of Sisal.

Specimens (2): ♂, 40783, testis 1 mm., 6.2 gm. (August 7), 1½ mi. S Sisal; ♂, 40784, testis 1 mm., 5.8 gm. starting to molt—1st and 2nd primaries ensheathed (August 10), 13 km. WSW Sisal.

Ramphocaenus rufiventris (Bonaparte): Long-billed Gnatwren.—Specimen (1): ♀, 40793, imm. skull, 9.8 gm. (July 15), 7½ km. W Escárcega.

Cyclarhis gujanensis insularis Ridgway: Rufous-browed Pepper-shrike.—Specimen (1): ♂, 40794, testis 2 mm., 37.8 gm., molting—4th primaries ensheathed (August 9), 4 km. N San Miguel, Isla Cozumel.

Vireo bairdii Ridgway: Cozumel Vireo.—Specimens (4): ♀, 40795, ovary inactive, 12.7 (August 8), ♂, 40796, testis 2 mm., 12.6 gm., molting—3rd and 4th primaries ensheathed (August 10), ♀, 40797, ovary inactive, 12.5 gm., molting—3rd primaries ensheathed (August 10), and ♂, 47098, imm., 13.1 gm. (August 10), from 2½-3½ km. N San Miguel, Isla Cozumel.

Vireo pallens semiflavus Salvin: Mangrove Vireo.—Paynter (1955a:236) noted breeding by this species from April 7 through June.

Specimens (2): ♀, 40800, ova to 3 mm., oviduct enlarged (July 8), Isla del Carmen; ♀, 40799, ovary inactive, 11.1 gm., molting—4th primaries ensheathed (August 2), Isla Mujeres.

Vireo flavoviridus flavoviridus (Cassin): Yellow-green Vireo.—Paynter's (1955a:238) data indicate breeding in this species from late May through June; our records indicate that the species breeds at least through July.

Specimens (12): ♂, 40812, testis 10 x 4 mm., 17.1 gm., molting—1st, 2nd, and 3rd primaries ensheathed (July 17), and ♂, 40813, testis 7 x 4 mm., 18.2 gm. (July 17), 1 km. N, 13 km. W Escárcega; ♀, 40803, ovary 9 x 5 mm., ova to 1 mm., brood patch (July 21), ♂, 40805, testis 11 x 6 mm., 18.5 gm. (July 21), ♂, 40804, 18 gm. (July 21), and ♀, 40802, ovary slightly enlarged, molting—2nd and 3rd primaries ensheathed (July 21), all from Pisté; ♂, 40806, 17.5 gm., molting—1st primaries ensheathed (July 21), 6½ km. W Pisté; ♀, 40808, ovary 5 x 3 mm., 17.4 gm. (July 28), ♂, 40807, testis 5 x 3 mm., 17.7 gm., molting—3rd and 4th primaries ensheathed (July 28), ♂, 40809, testis 2 x 1 mm., 17.5 gm. (July 29), and ♂, 40810, testis 3 x 2 mm., 18.7 gm., molting—1st, 2nd, 3rd, and 4th primaries ensheathed (July 30), from Pueblo Nuevo X-can; ♂, 40811, testis 3 x 1 mm., 18.7 gm., molting—4th, 5th, and 6th primaries and middle pair of rectrices ensheathed (August 14), 4 km. NNE Felipe Carrillo Puerto. Mallophaga: *Philopterus* sp. July 21.

Vireo magister (Lawrence): Yucatán Vireo.—Breeding on the peninsula has not been recorded previously. A male, beginning to molt, taken on August 10 on Isla Cozumel had enlarged testes, which were apparently regressing.

Specimens (3): ♀, 40814, ovary inactive, 17.7 gm. (August 2), Isla Mujeres; sex? 40815, 19.5 gm. (August 9), and ♂, 40816, testis 6 x 3 mm., 20.2 gm., molting—1st, 2nd, and 3rd primaries ensheathed (August 10), 3½ km. N San Miguel, Isla Cozumel.

Cyanerpes cyaneus carneipes (Sclater): Blue Honeycreeper. — Paynter (1955a:283) collected specimens that were breeding in April. Testes were fully enlarged in two August-taken specimens and courtship rituals were observed in two pairs seen on August 3 at Puerto Juarez.

Specimens (3): ♂, 40817, 15.5 gm. (July 21), 6½ km. W Pisté; ♂, 40818, testis 12 x 6 mm., 12.1 gm. (August 3), 4 km. WSW Puerto Juarez; ♂, 40819, testis 8 x 6 mm., 11.6 gm. (August 14), 4 km. NNE Felipe Carrillo Puerto.

Coereba flaveola caboti (Ridgway): Bananaquit.—Specimen (1): ♀, 40820, ovary inactive, 5 x 3 mm., 11.0 gm., molting—1st and 2nd primaries ensheathed, 3rd and 4th primaries missing (August 10), 3½ km. N San Miguel, Isla Cozumel.

Dendroica petechia rufivertex Ridgway: Yellow (Golden) Warbler. — Specimens (5): ♀, 40831, ovary inactive, 8.0 gm. (August 8), sex?, 40832, imm. (fresh, first winter plumage), 10 gm. (August 8), ♀, 40830, ovary inactive, 10.0 gm., molting—4th and 5th primaries ensheathed (August 9), ♀, 40833, ovary inactive, 8.5 gm. (August 9), and ♀, 40834, ovary inactive, 7.8 gm. (August 10), all from 3½-4 km. N San Miguel, Isla Cozumel.

Dendroica petechia bryanti Ridgway: Yellow (Mangrove) Warbler.—Previous records of breeding by this species are available for March 29 and 30 and May 16 (Paynter, 1955a:247). Breeding apparently continues at least

into July. An adult male with moderately enlarged testes (probably regressing) was taken on July 7 at Zacatel, Campeche, and a juvenile was obtained 13 km. WSW Sisal on August 10. The male at Zacatal was in mangroves alongside the ferry landing (for the ferry from Isla del Carmen) and seems to be the first specimen of this subspecies recorded for the state.

Specimens (7): ♂, 40829, testis 4 x 2 mm., 11.1 gm., molting—1st, 2nd, and 3rd primaries ensheathed (July 7), Zacatal, Campeche; ♂, 40823, imm., 10.0 gm. (August 9), ♂, 40824, testis 1 mm., 13.0 gm., molting—4th and 5th primaries and middle three rectrices ensheathed (August 9), ♂, 40826, juv., 10.1 gm. (August 10), ♂, 40827, imm. (fresh, first winter plumage), 10.2 gm. (August 10), sex?, 40825, 10.3 gm. (August 10), and ♂, 40828, testis 2 mm., molting—7th, 8th, and 9th primaries, 2nd, and 3rd secondaries and outer pair of rectrices ensheathed (August 11), all from 13 km. WSW Sisal.

Seiurus motacilla (Vieillot): Louisiana Waterthrush.—Our specimen, apparently an early migrant, was taken near the aguada at Rancho San Miguel.

Specimen (1): ♂, 40835, testis minute, 19.9 gm. (August 14), 4 km. NNE Felipe Carrillo Puerto.

Tangavius aeneus aeneus (Wagler): Red-eyed Cowbird.—A male having enlarged testes taken on August 14 seems to be the first record of breeding in the species for the peninsula.

Specimens (2): ♂, 40838, testis 11 x 7 mm., 66.9 gm. (August 14), and ♀, 40839, ovary 6 mm., 60 gm. (August 15), 4 km. NNE Felipe Carrillo Puerto.

Cassidix mexicanus (Gmelin): Boat-tailed Grackle.—Specimen (1): ♂, 40840, 223.3 gm. (July 9), 1 km. SW Puerto Real, Isla del Carmen.

Dives dives dives (Deppe): Sumichrast Blackbird.—This species previously has been known to breed in May (Paynter, 1955a:263). The specimens from July had moderately active ovaries.

Specimens (2): ♀, 40842, ovary 8 x 4 mm., 92 gm. (July 11), 5 km. SW Champotón; ♀, 40841, ovary 11 x 5 mm., 88.6 gm. (July 21), Pisté.

Icterus prosthemelas (Strickland): Black-cowled Oriole.—Specimens (2): ♀, 40843, ovary 5 x 3 mm., 28.8 gm., molting—extensive body molt, 1st, 2nd, and 3rd primaries ensheathed (August 3), 4 km. WSW Puerto Juarez; ♂, 40844, testis 2 x 1 mm., 31.0 gm., molting 1st, 2nd, 3rd, and 4th primaries ensheathed (August 16), 4 km. NNE Felipe Carrillo Puerto.

Icterus mesomelas (Wagler): Yellow-tailed Oriole.—Our specimens extend the known breeding season; previous records are for April and May (Paynter, 1955a:265).

Specimens (4): ♂, 40848, testis 11 x 5 mm. (July 14), 7½ km. W Escárcega; ♂, 40846, juv. (rectrices and remiges ensheathed basally), 30.3 gm. (July 29), and ♂, 40847, testis 12 mm., 38.0 gm. (July 29), Pueblo Nuevo X-can; ♀, 40845, ovary 6 x 3 mm., 32.5 gm. (August 4), 4 km. WSW Puerto Juarez.

Icterus auratus Bonaparte: Orange Oriole.—Paynter (1955a:266) reported breeding specimens taken in April and May. Two males taken in late July had fully enlarged testes.

Specimens (2): ♂, 40849, testis 10 x 6 mm., 32.5 gm. (July 28), Pueblo Nuevo X-can; ♂, 40850, testis 11 x 7 mm., 33.0 gm. (July 30), 1½ km. S, 1 km. E Pueblo Nuevo X-can.

Icterus gularis (Wagler): Black-throated Oriole.—Breeding in this species was reported by Paynter (1955a:267) only for the month of April. Breeding was apparently nearing an end in late July at Pisté, where several juveniles were taken. Adult males had moderately enlarged testes.

Specimens (8): ♂, 40858, testis 5 x 3 mm., 67.2 gm. (July 20), 6½ km. W Pisté; ♂, 40853, 59.0 gm. (July 21), ♀, 40851, imm., 49.9 gm. (July 21), ♂, 40852, 56.4 gm. (July 21), ♀, 40855, imm., 49.9 gm. (July 22), ♀, 40856, ovary inactive, 50.0 gm. (July 22), ♂, 40854, testis 6 x 4 mm., 63.8 gm. (July 22), and ♂, 40857, juv. (all rectrices and remiges ensheathed basally), 30.4 gm. (July 27), all from Pisté.

Icterus cucullatus Nelson: Hooded Oriole.—This species has not heretofore been recorded as breeding on Isla Cozumel; testes were nearly fully enlarged but probably regressing in the only specimen taken there. It had been banded (USF&WS no. 601-87003) on the island in 1961 as an adult. According to Paynter (1955a:269) there are no breeding records for this species on the mainland later than April, March 25 being the earliest date. The species was observed nesting on Isla del Carmen and adult males taken there and 5 km. S Champotón in early July were in full breeding condition.

Specimens (6): ♂, 40863, testis 11 x 7 mm., 26.3 gm. (July 8), ♀, 40864, 31.4 gm. (July 8), and ♂, 40862, testis 11 x 5 mm., 24.7 gm. (July 8), 1 km. SW Puerto Real, Isla del Carmen; ♂, 40860, 26.5 gm. (July 9), and ♂, 40861, testis 10 x 5 mm., 20.9 gm. (July 11); 5 km. S Champotón; ♂, 40859, testis 8 x 5 mm., molting—7th primaries ensheathed, 27.0 gm. (August 8), 3.5 km. N San Miguel, Isla Cozumel.

Tanagra affinis affinis Lesson: Lesson Euphonia.—Specimens (2): ♀, 40866, 8.8 gm. (July 22), Pisté; ♂, 40865, testis 3 x 2 mm., 10.0 gm. (August 3), 4 km. WSW (Aeropuerto) Puerto Juarez.

Tanagra lauta lauta Bangs and Penard: Thick-billed Euphonia.—According to Paynter (1955a:272), the only breeding record previously available is that of a male having slightly enlarged testes on February 12. Males taken on July 15 and on August 14 had fully enlarged testes; the gonads of several other specimens were apparently regressing, two specimens had begun to molt, and juveniles were molting into first winter plumage.

Specimens (9): ♂, 40874, testis 7 x 4 mm. (July 15), and ♀, 40875, ova to 1 mm. (July 15), 7½ km. W Escárcega; ♂, 40869, testis 6 x 4 mm., 14.5 gm. (August 14), ♂, 40870, testis 2 mm., 14.5 gm., molting—5th primaries ensheathed (August 14), ♂, 40867, imm., 12.6 gm. (August 14), ♀, 40868, imm., 14.4 gm. (August 14), ♂, 40871, testis 2 mm., 14.4 gm., molting—2nd, 3rd, and 4th primaries ensheathed (August 14), ♀, 40872, ovary granular, 7.8 gm. (August 14), and ♀, 40873, ovary granular, 13.0 gm. (August 15), all taken 4 km. NNE Felipe Carrillo Puerto.

Thraupis abbas (Deppe): Yellow-winged Tanager.—Paynter (1955a:273) reported breeding in this species in late April and late June. Gonads in our specimens were moderately active.

Specimens (2): ♂, 40877, testis 6 x 4 mm., 43.0 gm., molting—1st and 2nd primaries ensheathed (July 15), 1 km. N, 13 km. W Escárcega; ♀, 40876, ovary 7 x 4 mm., (ova to 1 mm.), 42.1 gm. (July 29), Pueblo Nuevo X-can.

Spindalis zena benedicti Ridgway: Stripe-headed Tanager.—Two males in advanced molt but with enlarged gonads were taken on August 9 and 10 and seem to be the first records indicating breeding in this species on Isla Cozumel.

Specimens (3): ♂, 40878, testis 9 x 7 mm., 32 gm., molting—5th primaries and middle pair of rectrices ensheathed (August 9), ♂, 40880, testis 5 x 3 mm., 30.0 gm., molting—3rd, 4th, 5th primaries and middle two pairs of restrices ensheathed (August 10), and ♀, 40879, ovary inactive, 28.1 gm., molting—remiges are new; secondary coverts ensheathed (August 10), 3½ km. N San Miguel, Isla Cozumel.

Piranga roseogularis (Cabot): Rose-throated Tanager.—Breeding has been previously recorded from March 17 through May 11 (Paynter, 1955a:276). Our only specimen, a male in advanced molt, had enlarged (regressing) testes.

Specimen (1): ♂, 40881, testis 7 x 5 mm., 24.2 gm., molting—4th and 5th primaries ensheathed (August 15), 4 km. NNE Felipe Carrillo Puerto.

Habia gutturalis (Sclater): Red-throated Ant-tanager.—The only breeding records previously available for this species on the peninsula are for May 18 (Paynter, 1955a:280) and June 25 (Paynter, 1955b). Specimens taken between July 14 and August 2 were in full breeding condition. A male (40882) and female (40883) taken 7½ km. W Escárcega were known to be mated. Plumages in all specimens are worn and for that reason specimens were not identified to subspecies.

Specimens (6): ♂, 40882, testis 14 x 9 mm., 38.9 gm. (July 14), ♀, 40883, ovary 5 x 5 mm., 29.0 gm. (July 14), and ♂, 40887, testis 10 x 7 mm. (July 16), 7½ km. W Escárcega; ♂, 40885, juv. (rectrices and remiges ensheathed basally) (July 28), and ♀, 40886, ovary moderately active, 30.5 gm., molting —2nd primaries ensheathed (July 28), Pueblo Nuevo X-can; ♂, 40884, testis 15 x 8 mm. (August 2), 4 km. WSW Puerto Juarez.

Saltator atriceps (Lesson): Black-headed Saltator.—Previously, breeding has been noted in this species in February, March, and April (Paynter, 1955a: 284). A male taken on July 16 was in full breeding condition.

Specimens (3): ♂, 40895, testis 15 x 9 mm., 80.4 gm. (July 16), and ♀, 40896, 73.5 gm. (July 17), 7½ km. W Escárcega; ♂, 40894, 71.6 gm. (July 29), Pueblo Nuevo X-can.

Saltator coerulescens (Vieillot): Gray Saltator.—The only previous breeding record for this species is for April 26. Our one specimen, No. 40897, a juvenal male barely able to fly, taken on July 21 at Pisté, weighed 43.8 grams.

Richmondena cardinalis (Linnaeus): Cardinal.—The only record of breeding previously reported is of a male with enlarged testes taken on June 4 (Paynter, 1955a:287). Adult males with enlarged testes were obtained on July 11 and August 10, and three juveniles were taken southwest of Sisal on August 10, 16, and 18.

Specimens (7): ♂, 40903, testis 9 x 7 mm., 39.7 gm. (July 11), and ♀, 40904, 34.0 gm. (July 11), 5 km. S Champotón; ♂, 40898, testis 7 x 4 mm., 33.8 gm. (August 10), and ♀, 40899, juv. (rectrices and remiges ensheathed basally), 32.8 gm. (August 10), 13 km. WSW Sisal; ♂, 40900, fledgling, 18.4 gm. (August 18), 2 km. WSW Sisal; ♀, 40901, ovary granular, 37.4 gm., molting—1st primaries ensheathed (August 15), and ♂, 40902, imm., 34.0 gm. (August 16), 4 km. NNE Felipe Carrillo Puerto.

Cyanocompsa parellina (Bonaparte): Blue Bunting.—Specimens (2): ♂, 40906, imm. (July 15), and ♂, 40905, testis 10 x 7 mm., 15.2 mm. (July 15), 7½ km. W Escárcega.

Tiaris olivacea pusilla Swainson: Yellow-faced Grassquit.—The only records of breeding, thus far, are by Paynter (1955a:291) for March 12 and June 14. A male (40907) taken 4 km. NNE Felipe Carrillo Puerto on August 14 had fully enlarged testes (8 x 5 mm.).

Tiaris olivacea intermedia (Ridgway): Yellow-faced Grassquit.—Although females taken on Isla Cozumel exhibited no reproductive activity, two males had moderately enlarged testes. These seem to be the first records of breeding in this subspecies, which is endemic to Isla Cozumel.

Specimens (5): ♂, 40908, testis 6 x 4 mm., 10.5 gm. (August 8), ♀, 40912, ovary inactive, 9.5 gm. (August 8), ♀, 40909, ovary inactive, 10.4 gm. (August 9), ♂, 40910, testis 5 x 3 mm., 11.5 gm., molting—1st primaries ensheathed (August 9), and ♂, 40911, 11.5 gm. (August 10), all from 2½-3½ km. N San Miguel, Isla Cozumel.

Sporophila torquiola morelleti (Bonaparte): White-collared Seedeater.—Breeding is known for this species in May and a male collected on September 2 was in breeding condition (Paynter, 1955a:293). Our records seem to be the first for the summer. Specimens taken in July and August were breeding.

Specimens (7): ♀, 40918, 9.2 gm. (July 8), 1 km. SW Puerto Real, Isla del Carmen; ♂, 40919, testis 7 x 6 mm., 8.2 gm. (July 15), 7½ km. W Escárcega; ♀, 40913, ovary inactive, 7.9 gm. (August 4), 4 km. WSW Puerto Juarez; ♂, 40914, testis minute, 7.8 gm. (August 14), ♀, 40915, ova to 6 mm. (August 15), ♀, 40917, ovary moderately active, 7.0 gm. (August 16), and ♂, 40916, testis 7 x 5 mm., 7.6 gm. (August 16), 4 km. NNE Felipe Carrillo Puerto.

Volatinia jacarina splendens (Vieillot): Blue-black Grassquit.—The only previous record of breeding is a male having slightly enlarged testes taken on June 1 (Paynter, 1955a:293). Our specimens showed various stages of reproductive activity when taken on July 10.

Specimens (6): ♂, 40926, 8.9 gm. (July 10), and ♂, 40925, testis 2 x 1 mm., 8.5 gm. (July 10), 1 km. S Puerto Real, Isla del Carmen; ♂, 40924, testis 4 x 2 mm. (July 10), ♂, 40922, testis 6 x 4 mm., 8.3 gm. (July 10), ♀, 40923, ova to 2 mm., 10.3 gm. (July 10), and ♂, 40921, 8.2 gm. (July 10), 5 km. S Champotón.

Arremonops rufivirgata verticalis Ridgway: Olive Sparrow.—Apparently the only previous record of breeding was the laying female on June 14 reported by Paynter (1955a:294). Males collected in July and August had enlarged testes; a juvenile, barely able to fly, was taken on August 14. Two specimens were beginning to molt.

Specimens (9): ♀, 40932, ova to 1 mm., 20.8 gm. (July 21), and ♂, 40933, testis 8 x 6 mm., 21.2 gm. (July 21), Pisté; ♀, 40930, ovary moderately active, 23.2 gm. (July 26), and ♂, 40931, imm., 22.7 gm. (July 26), 3½ km. N Pisté; ♂, 40934, testis 6 x 4 mm., 24.5 gm., molting—1st and 2nd primaries ensheathed (August 14), ♂, 40935, juv. (remiges and rectrices ensheathed basally), 17.7 gm. (August 14), ♀, 40936, imm., 25.0 gm (August 14), ♀, 40937, ovary granular, 22.6 gm., molting—2nd primaries ensheathed (August 15), and ♂, 40938, testis 7 x 5 mm. (August 15), 4 km. NNE Felipe Carrillo Puerto.

Arremonops chloronota chloronota (Salvin): Green-backed Sparrow.—Evidence presented by Monroe (1963) indicates that *A. chloronota* and *A. conirostris* are not conspecific. Specimens collected in breeding condition in July seem to be the first breeding records of this species on the peninsula.

Specimens (7): ♀, 40942, ova to 3 mm., 29.6 gm. (July 11), 5 km. S Champotón; ♂, 40944, testis 10 x 6 mm., 27.0 gm. (July 14), ♂, 40943, testis 5 x 3 mm., 23.1 gm. (July 14), and ♂, 40945, testis 7 x 4 mm., 25.5 gm. (July 15), 5-7½ km. W Escárcega; sex? 40939, 22.9 gm. (July 20), 6½ km. W Pisté; ♂, 40940, imm., 21.5 gm. (August 4), 4 km. WSW Puerto Juarez; ♀, 40941, 26.5 gm., extensive body molt, (August 15), 4 km. NNE Felipe Carrillo Puerto.

Table 2. An Alphabetical List of Species of Mallophaga Removed from Birds Collected on the Yucatán Peninsula in 1962.

Mallophaga	Hosts	KU Catalogue Nos. of specimens of hosts
Actornithophilus ochraceus	Snowy Plover	40426, 40431
Amyrisidea spicula	Chachalaca	Specimen not preserved
Austromenopon sachlebeni	Willet	40441
Carduiceps zonarius	Sanderling	40443, 40444
Ciconiphilus obscurus	American Egret	40402
Colpocephalum foetens	Black Vulture	Specimen not preserved
Colpocephalum megalops	King Vulture	40403
Columbicola macrourae	Zenaida Dove	40399
Columbicola sp.	Red-billed Pigeon	40457
Craspedorrhy sp.	Gray Hawk	40415
Lunaceps holophaeus actophilus	Sanderling	40444
Myrsidea sp.	Tropical Mockingbird	40771
Myrsidea sp.	Cave Swallow	40690, 40704
Myrsidea sp.	Sulphury Flat-billed Flycatcher	40685
Philopterus excisus	Cave Swallow	40697
Philopterus sp.	Sulphury Flat-billed Flycatcher	40682, 40686
Philopterus sp.	Great Kiskadee	40664
Philopterus sp.	Turquoise-browed Motmot	Specimen not preserved
Philopterus sp.	Yellow-green Vireo	40804
Penerirmus sp.	Red-capped Green Woodpecker	40594
Quadraceps assimilis major	Snowy Plover	40431
Quadraceps assimilis major	Wilson Plover	40432, 40436
Quadraceps carrikeri	Willet	40442
Quadraceps ravus	Spotted Sandpiper	40438
Quadraceps sp.	Laughing Gull	40449
Saemundssonia brevicornis	Cabot Tern	40452

SUMMARY

Locality records are given for each of 136 species of birds represented by 493 specimens and sight records are given for eight additional species.

The Yellow-headed Vulture is reported apparently for the first time from the peninsula. The specimens of the Streak-headed Woodhewer and the Louisiana Waterthrush are the second ones of each species taken on the peninsula. The Purple Martin taken on August 14, the Barn Swallow on August 18, and the Louisiana Waterthrush on August 14 represent earliest known autumn dates for these transients.

Evidence for breeding is given for 20 species for the first time and extensions of the known breeding seasons are presented for 41 species.

Fourteen genera, representing about 19 species, of Mallophaga are reported for 20 different species of bird hosts.

At Pisté and Puerto Juarez, species of birds such as the Blue Honeycreeper and the Red-capped Manakin, normally thought of as characteristic of more humid areas, were found breeding in numbers near *cenotes*. However, they were not seen to venture far into the surrounding deciduous forest. The availability of suitable habitat brought on by the rainy season and the regular occurrence of *cenotes* helps to explain the presence of such species far outside the Rain Forest zone.

LITERATURE CITED

BLAKE, E. R.
1953. Birds of Mexico a guide for field identification. Univ. of Chicago Press, Chicago, xxix + 644 pp.

BRODKORB, P.
1943. Birds from the gulf lowlands of southern Mexico. Misc. Publ., Mus. Zool., Univ. Michigan., 55:1-88, January 30.

FRIEDMANN, H., GRISCOM, L., and MOORE, R. T.
1950. Distributional check-list of the birds of Mexico Part I. Pac. Coast Avif., 29:1-202, June 30.

JOHSTON, R. F.
1962. The taxonomy of pigeons. Condor, 64:69-74, January 30.

LOWERY, G. H., JR. and BERRETT, D. G.
1963. A new Carolina Wren (Aves: Troglodytidae) from southern Mexico. Occas. Papers Mus. Zool., Louisiana St. Univ., 24:1-3, December 20.

MILLER, A. H., FRIEDMANN, H., GRISCOM, L., and MOORE, R. T.
1957. Distributional check-list of the birds of Mexico Part II. Pac. Coast Avif., 33:1-436, December 20.

MONROE, B. L., JR.
1963. Notes on the avian genus *Arremonops* with description of a new subspecies from Honduras. Occas. Papers Mus. Zool., Louisiana St. Univ., 28:1-12.

PAYNTER, R. A., JR.
1955a. The ornithogeography of the Yucatán Peninsula. Bull. Peabody Mus. Nat. Hist., 9:1-347.
1955b. Additions to the ornithogeography of the Yucatán Peninsula. Postilla, no. 22, 4 pp. (unpaged).

RIDGWAY, R.
1914. Birds of North and Middle America: a descriptive catalogue . . . Bull. U. S. Nat. Mus., 50:xx+1-882, 35 pls., April 8.

SELANDER, R. K. and GILLER, D. R.
1963. Species limits in the woodpecker genus *Centurus* (Aves). Bull. Amer. Mus. of Nat. Hist., 124:215-273.

SKUTCH, A.
1947. Life history of the turquoise-browed motmot. Auk, 64:201-217, April.

STORER, R. W.
1961. Two collections of birds from Campeche, Mexico. Occas. Papers Mus. Zool., Univ. Michigan, 621:1-20, August 15.

TRAYLOR, M. A., JR.
1941. Birds from the Yucatán Peninsula. Publ. Field Mus. Nat. Hist., Zool. Ser., 24:195-225.

WEBSTER, J. D.
1963. A revision of the rose-throated becard. Condor, 65:383-399, 3 figs., 8 tables, September 27.

WETMORE, A.
1950. The identity of the American vulture described as *Cathartes burrovianus* by Cassin. Jour. Wash. Acad. Sci., 40:415-417.

Transmitted July 11, 1967.

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Morphological Variation in a Population of the Snake, Tantilla gracilis Baird and Girard

BY

LAURENCE M. HARDY AND CHARLES J. COLE

University of Kansas
Lawrence
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Morphological Variation in a Population of the Snake, Tantilla gracilis Baird and Girard

By

LAURENCE M. HARDY AND CHARLES J. COLE

INTRODUCTION

Variation of selected taxonomic characteristics of flat-headed snakes (*Tantilla gracilis* Baird and Girard) from several midwestern states was studied by Force (1935), but she did not attempt a comprehensive evaluation. Taylor (1936) reported on variation in *T. gracilis* from various localities in Kansas; Kim, Burger, and Smith (1949) studied selected structures of specimens of *T. gracilis* from throughout its range. The present study was undertaken to determine the variation in both currently used and potential taxonomic characteristics of *T. gracilis* from one locality.

We are thankful to Charles W. Myers, Gorgas Memorial Laboratory, for suggestions concerning characteristics examined. We are indebted to Drs. William G. Degenhardt, University of New Mexico, Herndon G. Dowling, New York Zoological Society, Charles H. Lowe, University of Arizona, and Richard G. Zweifel, American Museum of Natural History, for criticizing the manuscript. Dr. William E. Duellman permitted us to study specimens in the University of Kansas Museum of Natural History.

Materials and Methods

The specimens examined were donated to the Museum of Natural History, University of Kansas, by the late Paul Anderson of Independence, Missouri. All specimens (KU numbers 83435-83680; N = 246) were collected in the vicinity of Winfield, Cowley County, Kansas, by Charles E. Burt and students from Southwestern College in the period from 1938 to 1941, inclusive.

Both authors gathered data on most characteristics and examined each atypical individual. Hardy determined characters of the maxillae (which were removed; N = 20), body and total lengths, and the scale formula of KU 83620.

We examined 22 characteristics of external morphology and 10 of the maxillae. All paired characteristics (excepting those of the maxillae) were examined on both sides of each snake and are referred to from the left side to the right side (for example, "preoculars 1-2" means there is one preocular on the left side and there are two on the right). Oviducts and oviducal eggs were observed on specimens designated as females; hemipenes were examined on specimens designated as males. Total length was measured by straightening each snake along a 300 mm. scale. Tail length was measured only on snakes having complete tails, and body length (snout-vent) was considered as total length minus tail length. The body length was measured on snakes having incomplete tails.

Supralabials, infralabials, preoculars and postoculars were counted, and we followed Peters (1960:9) in determining the nature of the temporals. Occasionally the primary (anterior) temporal is separated from the postocular by contact of the parietal and a supralabial (Taylor, 1936:338). We followed Peters (1964:219-220) in determining characteristics of the nasal and we looked for contact of the prefrontal with particular supralabials (Taylor, 1936:338). We determined which supralabials are in contact with the eye and whether the mental is in contact with the anterior pair of chin-shields.

The number of rows of dorsal scales was determined at five locations: a) around the neck—counts were made from each side diagonally and posteriorly from the anteriormost dorsal scale in contact with the first ventral (see below)—counts from the left and right sides are the first and second counts, respectively, recorded in the scale formula; b) one head length posterior to head—counts were made either diagonally and posteriorly or in a zig-zag pattern, beginning at the end of the second count around the neck—this is the third count recorded in the scale formula; c) midbody (approximated)—counts were made either diagonally and posteriorly or in a zig-zag pattern—this is the fourth count in the scale formula; d) anterior to anus (preanal)—counts were made in a zig-zag pattern beginning on one side and ending on the other at the first dorsal scale in contact with the anal plate—this is the fifth count in the scale formula.

We followed the method of Dowling (1951:98-99) in counting ventrals, and the anal plate was determined as entire, divided, or partly divided. Subcaudals were counted on only the right side beginning at the first scale that contacts a corresponding scale from the opposite side; fusion of particular pairs of subcaudals was determined. The "spine" at the tip of the tail was not counted. The head scutellation of each specimen was examined for abnormalities.

We determined the number of fangs and the number of maxillary teeth anterior to them and recorded the presence or absence of a diastema between the anterior fang and the maxillary tooth immediately preceding it. The diastema, if present, is a space distinctly wider than the spaces separating the prediastemal teeth.

The point of intersection of two perpendicular lines of an ocular grid determined which tooth-socket occurs directly opposite the distal tip of the suborbital process (Fig. 5b), but if that point occurs between two sockets then the number recorded was the number of the tooth immediately anterior to that point plus one-half.

The anterior and posterior edges of the suborbital process were determined as parallel or not at any point by aligning them with parallel lines on an ocular grid (Fig. 5b).

The angle of the posterior edge of the lateral flange was determined as an acute, obtuse, or right angle by fitting it to a pair of perpendicular lines of an ocular grid (Fig. 5b).

The number of lateral anterior foramina (Fig. 4b) was determined. If only two are present, their lengths (anterior to posterior) were compared by measuring them with an ocular micrometer. Also, if two lateral anterior foramina are present, the point of intersection of two perpendicular lines of an ocular grid determined which tooth-socket occurs directly below the center of the posterior foramen (Fig. 4b).

RESULTS

General Characteristics

From the data given by Force (1935), Taylor (1936), and Kirn *et al.* (1949), and from our own data, we conclude that a typical specimen of *gracilis,* meaning a specimen having the usual characteristics of the species, has the following characteristics in combination: supralabials 6-6; infralabials 6-6; preoculars 1-1; postoculars 1-1; temporals 1 + 1 on each side; nasal divided below naris; supralabials 3 + 4 entering orbit; mental in contact with chin-shields; all five dorsal scale counts 15; anal plate divided. (In the present work we use the words usual, unusual, typical, and atypical with neither quotation marks nor apology).

Of the 244 specimens on which we could examine each of these characteristics, only 125 (51.2%) have all of the typical characteristics in combination. The 119 specimens that do not possess all of the typical characteristics in combination include 31 (12.7% of the 244) that lack at least two of the typical characteristics.

Sex

The sample (N = 246) is composed of 107 (43.5%) females and 139 (56.5%) males.

Measurements

Females have total lengths from 96 to 244 mm. (mean, 173.3; N = 79). One female (KU 83480) measuring 244 mm. may be the longest specimen known (Conant, 1958, reports the longest as 9⅝ inches—approximately 232 mm.). Males have total lengths from 96 to 215 mm. (mean, 162.4; N = 109). Females have tail lengths from 16 to 50 mm. (mean, 34.6; N = 79), and males have tail lengths from 21 to 53 mm. (mean, 37.8; N = 109).

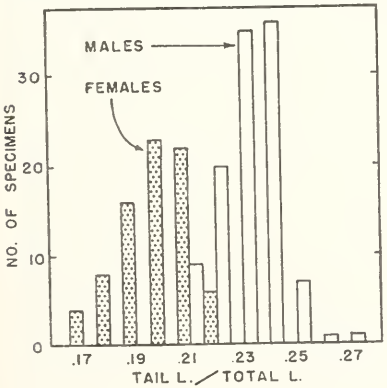

FIG. 1. Ratio of tail length to total length in females and males of *T. gracilis.*

The ratio of tail length to total length in females is from 0.17 to 0.22 (mean, 0.20; N = 79); in males it is from 0.21 to 0.27 (mean, 0.23; N = 109; Fig. 1). Juveniles (those less than 125 mm. in total length according to Force, 1935: tables 1 and 2) have proportionally shorter tails than do adults; the ratio of tail length divided by total length is 0.17-0.21 (mean, 0.18; N = 14) in females and 0.21-0.23 (mean, 0.22; N=16) in males. Adult females (125 mm. or more in total length) have ratios from 0.18 to 0.22 (mean, 0.20; N = 65) and adult males have ratios from 0.21 to 0.27 (mean, 0.23; N = 93).

Of the 246 specimens examined, 58 have incomplete tails. Of these 58 specimens, six had freshly broken tails, so we assume that 52 (21.1% of the 246) have incomplete tails resulting from natural causes; the remaining six specimens

could have had their tails broken at or soon after capture, assuming that none of the snakes was retained in captivity for an extended period.

Supralabials

The supralabials are either six (usually) or seven on a side (Table 1). When seven supralabials are present on either one or both sides, the addition results from one of the following conditions: a) 5 is divided to form 5 and 6 (N = 6); b) 2 and 3 form 2, 3, and 4 (N = 1); c) 5 and 6 form 5, 6, and 7 (N = 12); d) 4, 5, and 6 form 4, 5, 6, and 7 (N = 1); e) 1 and 2 form 1, 2, and 3 (N = 1); f) 1, 2, and 3 form 1, 2, 3, and 4 (N = 1); g) 2 is fused with the nasal, and 3 and 4 are reduced to granules (N = 1); h) type of addition unknown (N = 5).

TABLE 1. Variation in Number of Supralabials (N = 245) and Infralabials (N = 246) of Tantilla gracilis.

Number of Supralabials	Number of specimens	Per cent of occurrence	Number of infralabials	Number of specimens	Per cent of occurrence
6–6	221	90.2	5–5	5	2.0
6–7	10	4.1	5–6	4	1.6
7–6	10	4.1	6–5	5	2.0
7–7	4	1.6	6–6	229	93.1
			6–7	1	0.4
			7–6	2	0.8

In three of the four specimens with 7-7 supralabials, the type of addition is the same on each side, whereas the other specimen has a different type of addition on each side. Of the 23 examples for which the type of addition is known, 19 (82.6%) have the increase in number on the posterior half of the series.

In one specimen the third supralabial on the right is diagonally divided and the resulting upper part does not contact the edge of the lip; hence the specimen has 6-6 supralabials.

Infralabials

The infralabials are five, six (usually), or seven on a side (Table 1). When five infralabials are present on either one or both sides, the reduction results from one of the following conditions: a) 2 and 3 are fused (N = 3); b) 1, 2, and 3 form 1 and 2 (N = 6); c) 2, 3, and 4 form 2 and 3 (N = 3); d) 5 is separated from the edge of the lip by a projection from an adjacent infralabial (N = 1); e) 1, 2, 3, and 4 form 1, 2, and 3 (N = 2); f) type of reduction unknown (N = 4).

Of the specimens with 5-5 infralabials, two have the same type of reduction on each side, one has a different type of reduction on each side, and the type of reduction is unknown for the other two specimens.

When seven infralabials are present on either one or both sides, the addition can result from infralabials 2 and 3 forming 2, 3, and 4 (N = 2); the type of addition is unknown in one specimen.

In one specimen the second infralabial on the right side is reduced to a small wedge-shaped granule and in another specimen several infralabials on both sides are irregularly divided horizontally, although both specimens have six infralabials on the sides having the abnormalities.

Preoculars

Of the 245 specimens examined, 242 (98.8%) have one preocular on each side. Both preoculars are absent from two specimens, and one specimen has 1-0. In each case when a preocular is lacking, the "preocular" and prefrontal are fused. One specimen having 1-1 preoculars has both of them reduced to small vertical slivers.

Postoculars

Of the 245 specimens examined, 242 (98.8%) have one postocular on each side. Postoculars are 2-1 in two specimens and 1-2 in one. In one specimen the lower of the two postoculars on each side is very small, being approximately ⅓ the diameter of the upper one (measured with an ocular micrometer).

Temporals

Of the 245 specimens examined, 235 (95.9%) have 1 + 1 temporals on each side. Four specimens exhibit addition of temporals: one specimen has two secondary temporals on the left, and one has a tertiary temporal on the left. Two specimens have partly healed head injuries that probably caused atypical temporal conditions: one specimen has two primary temporals on the left, and one has two secondary temporals on the left and two upper and one lower secondary temporal on the right.

Six specimens exhibit reduction of temporals: one lacks a primary temporal on the left ("temporal" is fused with sixth supralabial), two lack secondary temporals on the right, and three lack secondary temporals on the left. The right secondary "temporal" of one specimen is separated from the supralabials by a posterior extension of the primary temporal.

Of the 246 specimens examined, 200 (81.3%) have both primary temporals in contact with their adjacent postoculars. Thirteen specimens (5.3%) have only the left primary temporal in contact with the postocular and eight (3.3%) have only the right primary temporal in contact with the postocular. Twenty-five specimens (10.2%) have both primary temporals separated from the postoculars. Separation of the primary temporal from the postocular, whenever it occurs, results from contact of mutual extensions from the adjacent parietal and supralabial (usually the fifth).

Nasal

Of the 243 specimens examined, 237 (97.5%) have the nasal divided below the naris on both sides. Three specimens have the nasal completely divided (above and below the naris) on only the left side; one specimen has a completely divided nasal on only the right side. A groove, but not a complete division of the nasal, is present above the left naris of one specimen. One specimen lacks the typical division below the naris on both sides, but a complete suture is present posterior to the naris and the resulting postnasal scales are, according to position, loreals.

Contact of prefrontal with supralabials

Of the 243 specimens examined, 147 (60.5%) have the prefrontal separated from the labials on each side. Of the remaining 96 specimens, 53 (21.8% of the 243) have the prefrontals in contact with the second labial on each side; five other variations of this characteristic were observed (Table 2).

TABLE 2. Variation in Contact of the Prefrontals and the Labials in 243 Specimens of Tantilla gracilis.

CHARACTERISTIC	Number of specimens	Per cent of occurrence
No contact	147	60.5
Contact of prefrontal with second labial on right	26	10.7
Contact of prefrontal with second labial on left	10	4.1
Contact of prefrontal with each second labial	53	21.8
Contact of prefrontals with labial two on left and labial three on right	1	0.4
Contact of prefrontals with labial three on left and labial two on right	3	1.2
Contact of prefrontals with labial two on left and labials two and three on right	3	1.2

The specimen having the prefrontal in contact with labial 2 on the left and labial 3 on the right has seven supralabials on the right, the extra labial being added anterior to the eye. In two of the three specimens with the prefrontals in contact with labial 3 on the left and labial 2 on the right, the preoculars and prefrontals are fused on each side; the third specimen has each preocular reduced to a small vertical sliver. Of the three specimens having the prefrontals in contact with labial 2 on the left and labials 2 and 3 on the right, two are typical with respect to other characteristics that might result in this atypical condition, but one has the prefrontals and preoculars fused.

Supralabials entering orbit

Of the 246 specimens examined, 233 (94.7%) have the third and fourth supralabials entering each eye (Table 3). All snakes that have the fourth and fifth labials entering the orbit on either side also have seven supralabials on the same side. One specimen having only the fourth labial entering the eye on the right side also has six supralabials on that side, but the third supralabial is split diagonally and the part contacting the eye does not contact the lip and hence is not a supralabial. The remaining three atypical conditions ($4/3+4$; $3+4/3+4+5$; $3+4+5/3+4$) occur only one time each and on snakes having 6-6 supralabials.

Contact of mental with chin-shields

Of the 246 specimens examined, 190 (77.2%) have the mental in contact with both anterior chin-shields. The mental is in contact with only the left anterior chin-shield in 15 specimens, only the right anterior chin-shield in 2

TABLE 3. Variation in Number of Supralabials Entering the Eye in 246 Specimens of Tantilla gracilis.

SUPRALABIALS		Number or specimens	Per cent of occurrence
Left	Right		
3 + 4	3 + 4	233	94.7
4 + 5	3 + 4	4	1.6
4	3 + 4	1	0.4
3 + 4	4 + 5	5	2.0
3 + 4	4	1	0.4
3 + 4	3 + 4 + 5	1	0.4
3 + 4 + 5	3 + 4	1	0.4

specimens, and the mental does not contact either anterior chin-shield in 39 specimens. Separation of the mental and an anterior chin-shield always results from the posterior elongation of a first infralabial.

Dorsal scale rows

Of the 245 specimens examined for this characteristic, 228 (92.7%) have scale counts of 15-15-15-15-15. The number of scale rows around the neck and one head length behind the head are 15 except in a single specimen that has 14 scale rows at these three places. The number of scale rows around midbody is 15 in 244 of 246 specimens (99.2%); two specimens have 14 scale rows around midbody. The number of preanal scale rows is more variable; counts of 14 through 17 were recorded. Fourteen specimens have 14 preanal scale rows (5.7%), 229 have 15 preanal rows (93.1%), two have 16 preanal rows (0.8%), and one has 17 preanal rows (0.4%). Known causes for atypical numbers of preanal scale rows are listed in Table 4. A preanal count at one head length anterior to the anus would have omitted most of the above variation in numbers of preanal scale rows.

TABLE 4. Atypical Numbers of Preanal Scale Rows in Specimens of Tantilla gracilis.

Preanal scales	Number of specimens	CAUSE	Per cent of occurrence
14	10	Scale rows seven and eight on left fuse within the last five ventrals	4.1
14	1	Scale row two on the right is lost adjacent to the penultimate ventral	0.4
16	1	Scale row eight on the left divides adjacent to the last ventral	0.4
16	1	A scale row is added on the right adjacent to and anterior to the anal plate	0.4
17	1	A scale row is added on each side adjacent to and anterior to the anal plate	0.4

The complete dorsal scale formula for KU 83620, a male, is as follows:

$$15\ \frac{6+7(2)}{6+7(2)}\ 13\ \frac{+7(4)}{}\ 14\ \frac{}{+7(5)}\ 15\ \frac{6+7(11)}{6+7(11)}\ 13\ \frac{}{6=6+7(17)},$$

$$14\ \frac{}{6+7(18)}\ 13\ \frac{}{+7(25)},$$

$$14\ \frac{+7(26)}{}\ 15\ \frac{}{6+7(36)}\ 14\ \frac{6+7(38)}{}\ 13\ \frac{+7(39)}{}\ 14\ \frac{}{+7(42)},$$

$$15\ \frac{}{-6(45)}\ 14\ \frac{}{+7(53)},$$

$$15\ \frac{7+8(67)}{}\ 14\ \frac{+7(69)}{}\ 15\ \frac{}{6+7(90)}\ 14\ \frac{}{+7(93)}\ 15\ \frac{}{6+7(99)},$$

$$14\ \frac{}{+7(100)}\ 15(122).$$

Specimen 83620 is the only one for which we have determined the complete dorsal scale formula. Obviously the formula is complex, and possibly the specimen is atypical in this regard. Nevertheless, addition and reduction of scale rows is apparent on other specimens and can be easily observed by examining specimens under a dissection microscope.

Anal plate

Of the 246 specimens examined, 232 (94.3%) have the anal plate divided. Of the 14 specimens having undivided anal plates, four have an incomplete groove anteriorly in the plate.

Ventrals

Females have from 122 to 137 (mean, 130.8 ± 0.26; $N = 107$) ventrals; males have from 117 to 131 (mean, 122.3 ± 0.21; $N = 139$; Fig. 2). Of the 246 specimens examined, 29 (11.8%; 11 females and 18 males) have an added

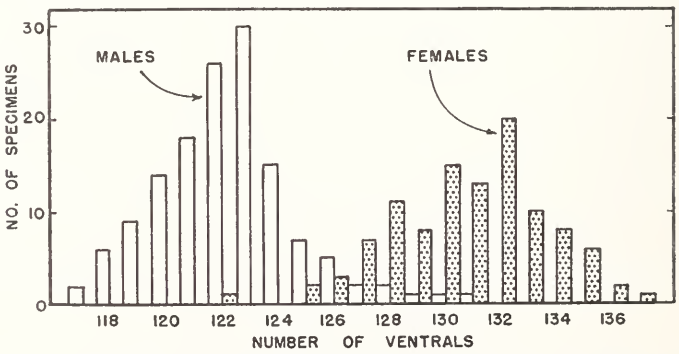

FIG. 2. Number of ventrals in females and males of *T. gracilis*.

half-ventral immediately anterior to the anal plate. Of these specimens, 27 have the added half-ventral on the left side and two have it on the right. Five specimens have the last ventral divided similar to the normal division of the anal plate. One specimen has the last ventral incompletely divided transversely. Excluding the last ventral, seven specimens have divided ventrals (half-ventrals). Four of these specimens have added half-ventrals on the right side (two specimens with one half-ventral each, one specimen with two half-ventrals, and one specimen with three half-ventrals), and four have added half-ventrals on the left side (one half-ventral on each specimen).

Subcaudals

Females have from 37 to 47 (mean, 42.0 ± 0.20; $N = 79$) subcaudals; males have from 43 to 55 (mean, 48.4 ± 0.23; $N = 109$; Fig. 3). Of the 187 specimens examined, 13 (7.0%) have the last pair of subcaudals fused. One specimen has left subcaudal 28 fused with both adjacent subcaudals (also fused) on the right. While reading proof we found two omissions in Fig. 3; there should be illustrated two males with 43 subcaudals and three males with 44 subcaudals.

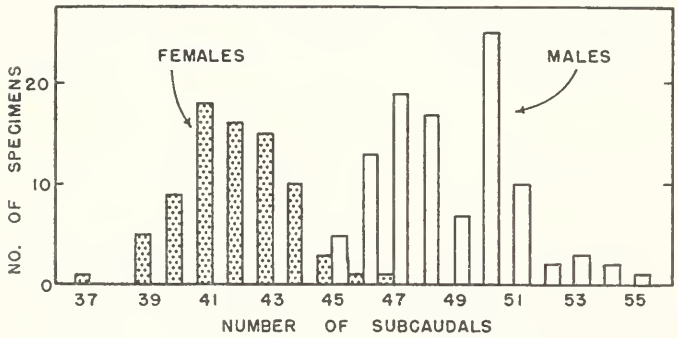

Fig. 3. Number of subcaudals in females and males of *T. gracilis*.

Ventrals minus subcaudals

The value for number of ventrals minus the number of subcaudals varies from 80 to 96 (mean, 88.8 ± 0.39) for 79 females, and from 67 to 83 (mean, 73.8 ± 0.28) for 109 males.

Additional scale characteristics

Of the 246 specimens examined, four (1.6%) have the rostral in contact with the left prefrontal, and hence the internasals are separated from one another. One snake has approximately one-fourth (anteriorly) of the suture between the parietals fused. One specimen has the posterior edge of the frontal fused with the left parietal. One specimen has the parietal shield on the right side abbreviated posteriorly. One specimen has both prefrontals fused with the frontal, although an incomplete suture is present.

Maxillary characteristics (*Figs. 4 and 5*)

Maxillary teeth anterior to fangs 10-14 (mean, 12.1; N = 20); tooth-socket number 6.5-8.5 (mean, 7.2; N = 20) directly opposite distal tip of suborbital process; lateral anterior foramina 1-3 (mean, 1.8; N = 20); tooth number 6-9 (mean, 6.9; N = 12) directly below center of posterior foramen (if only two foramina present). Three specimens lack a diastema and 17 specimens have a diastema. The anterior and posterior edges of the suborbital process are parallel in two specimens and not parallel in 14; the process is broken in four specimens. The lengths (anterior to posterior) of the lateral anterior foramina (if only two are present) are approximately equal in six specimens, and in six the anteriormost one is the longest; six specimens have one foramen and two specimens have three foramina. All specimens examined have two fangs, with the posterior edge of the lateral flange forming an obtuse angle.

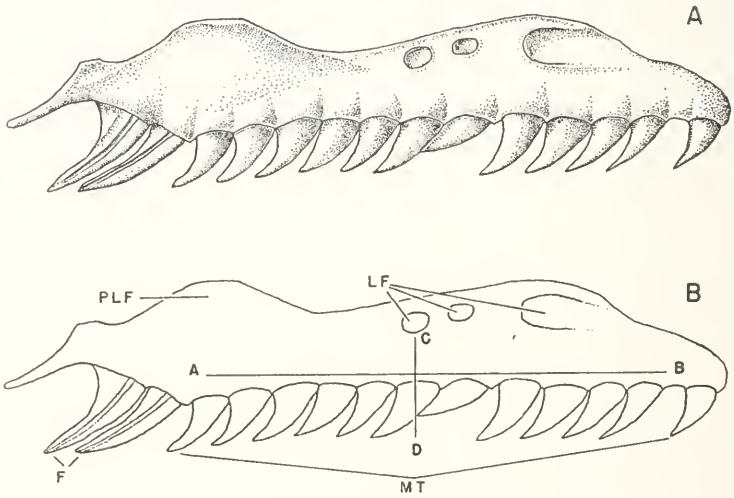

FIG. 4. Lateral view of right maxilla of *T. gracilis* (KU 83484), × 39. Actual length of bone is 2.44 mm. A. Detail of bone. B. Outline sketch of bone to illustrate characteristics examined. Lateral anterior foramina (LF); fangs (F); "prediastemal" maxillary teeth (MT); lateral flange (PLF); perpendicular lines, A-B and C-D, are used to determine which tooth-socket occurs directly below the center of the posterior foramen (the specimen illustrated is atypical because there are three foramina present).

Discussion and Conclusions

Generic characteristics of *Tantilla* are as follows: size small, body slender, head not noticeably distinct from body; preoculars one; postoculars one or two; nasals two; loreal absent; smooth dorsal scales in 15 rows; anal plate usually divided but sometimes single; subcaudals paired; usually two enlarged, posterior, grooved fangs on the maxilla separated by a small diastema from the other maxillary teeth (Baird and Girard, 1853:131; Cope, 1900:1110; Dunn, 1928:24; Blanchard, 1938:369; Schmidt and Davis, 1941:268; Wright and Wright, 1957:722; Conant, 1958:180). Of these characteristics, only the fol-

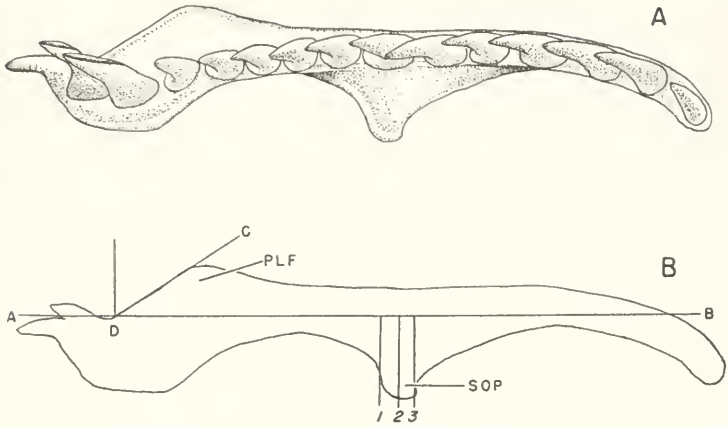

FIG. 5. Ventral view of right maxilla of *T. gracilis* (KU 83484), × 39. Actual length of bone is 2.44 mm. A. Detail of bone. B. Outline sketch of bone to illustrate characteristics examined. Lateral flange (PLF) forms an obtuse angle (ADC) with main axis of bone (AB); a reference line (2), perpendicular to the main axis of the bone, is used to locate the tooth-socket directly opposite the tip of the suborbital process (SOP); the anterior and posterior edges of the suborbital process are not parallel at any point (reference lines 1 and 3).

lowing were invariable in our sample: size small, body slender, head not noticeably distinct from body; postoculars one or two; smooth dorsal scales; posterior grooved fangs on maxilla. The dorsal scales, anal, and subcaudals were "correct" 92 percent of the time; the preoculars and nasals were "correct" 97 per cent of the time.

Tantilla reportedly has two nasals (Baird and Girard, 1853:131; Cope, 1900:1110; Wright and Wright, 1957:722). *Tantilla gracilis* usually has a single nasal that is divided below the naris; variation in this characteristic is discussed above.

In addition to the generic characteristics, specific characteristics for *T. gracilis* are as follows: supralabials 5-8 (usually 6); supralabials 3 and 4 entering orbit; infralabials 5-7 (usually 6); temporals 1 + 1; ventrals 115-138 in females, 106-132 in males; subcaudals 33-53 in females, 40-57 in males; tail length 13-27 per cent total length in females, 15-30 per cent in males (Baird and Girard, 1853:132; Cope, 1900:1111-12; Force, 1935:653-54; Taylor, 1936: 337-38; Blanchard, 1938:371-72; Kirn, Burger, and Smith, 1949:240-49). Excepting the number of temporals and the supralabials entering the orbit, the characteristics of the specimens in our sample are within the ranges of variation mentioned above. Of the 10 maxillary characteristics studied, no variation was observed in number of fangs or angle of lateral flange.

Because our data have some bearing on the problem of geographic variation in *T. gracilis* and the recognition of subspecies, we comment briefly on the status of subspecies in *T. gracilis*. Kirn, Burger and Smith (1949) proposed the recognition of two subspecies of *Tantilla gracilis* (*T. g. gracilis* Baird and Girard and *T. g. hallowelli* Cope). These subspecies were diagnosed on the

basis of differences in ventrals, subcaudals, and the ratio of tail length to total length; sexual dimorphism in each characteristic was considered. We do not recognize these subspecies for the reasons given below.

The data of Kirn *et al.* (1949) appear to be presented inaccurately in part. Both of us independently recalculated the mean given for each characteristic for each subspecies, using the data in figures 2-4 of Kirn *et al.* (1949:242, 244-245). Of their 12 means presented (table 1, p. 247) only two agree with our recalculated means, although the means calculated by each of us independently are in complete agreement (Table 5). Also, we independently calculated the percentages of specimens of each "subspecies" that are included in the ranges of variation given in their diagnoses (Table 5); again, our independent calculations are in complete agreement. In our opinion the differences between the populations for the characteristics analyzed do not warrant recognition of subspecies (Fig. 6).

TABLE 5. Means of "Diagnostic" Characteristics of T. g. gracilis Baird and Girard and T. g. hallowelli Cope.

CHARACTERISTICS	*T. g. gracilis*			*T. g. hallowelli*		
	Mean (Kirn, *et al.* 1949)	Mean (Kirn, *et al.*) recalculated by us	Per cent specimens of Kirn, *et al.* included in their diagnosis	Mean (Kirn, *et al.* 1949)	Mean (Kirn, *et al.*) recalculated by us	Per cent specimens of Kirn, *et al.* included in their diagnosis
Ventrals—females	125.67	125.71	69.4	130.07	130.07	79.6
Ventrals—males	115.97	116.61	70.0	121.22	120.87	69.7
Caudals—females	40.99	40.82	62.8	46.79	43.82	77.4
Caudals—males	47.75	48.29	78.3	51.67	50.29	51.0
Tail L./total L. females	.1976	.1976	69.0	.2084	.2076	74.2
Tail L./total L. males	.2336	.2362	56.1	.2477	.2423	79.6

The data presented by Kirn *et al.* do not demonstrate intergradation between two populations. Moreover, the diagnostic ranges of the number of subcaudals in males of *hallowelli* and the ratio of tail length to total length in males of *gracilis* do not include the recalculated means for those characteristics. Furthermore, the means for the following characteristics are dangerously close to being excluded from their respective "diagnostic" ranges: in *hallowelli*, the number of ventrals in males; in *gracilis*, the number of subcaudals in females, and the ratio of tail length to total length in females. It is incongruous that Kirn *et al.* state (p. 243) that "the coefficient of geographic divergence is .6 per degree latitude" for ventrals, and on the same page they state that "The average number of ventrals gradually increases toward the north in *Tantilla gracilis* except in southern Oklahoma and central Arkansas (the area of intergradation between *T. g. gracilis* and *T. g. hallowelli*) where the change seems to be more abrupt." The data presented in Kirn *et al.* (1949) do not demonstrate an abrupt change.

The present sample of *T. gracilis* from Kansas is clearly within the geographic range of *T. g. hallowelli* as mapped by Kirn *et al.* (1949:241). How-

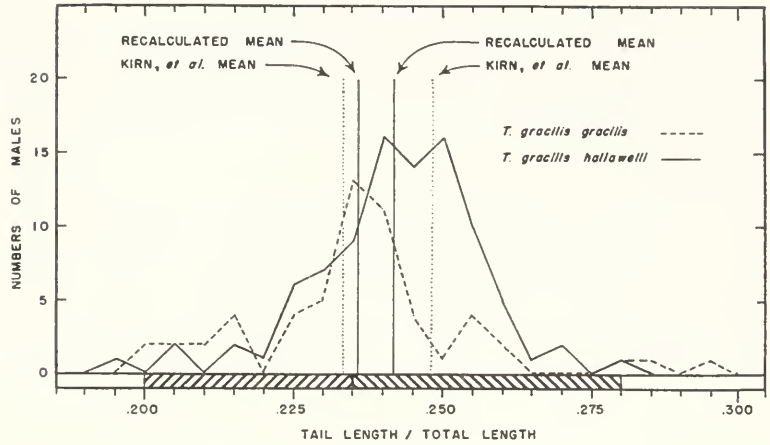

FIG. 6. Frequency polygons presenting ratios of tail length to total length for males of *T. g. gracilis* and *T. g. hallowelli* from Kirn, *et al.* (1949). The dotted vertical lines represent the means given by Kirn, *et al.* (1949) for *gracilis* (left) and *hallowelli* (right); the solid vertical lines represent the recalculated means for *gracilis* and *hallowelli*, respectively, using the data of Kirn, *et al.* The hatched bars represent the range included by Kirn, *et al.* (1949) in their diagnoses of *gracilis* (left) and *hallowelli* (right).

ever, for the sample from Kansas, the mean number of subcaudals of males is well within the diagnostic range for *T. g. gracilis* (Table 6), the mean number of subcaudals of females is closer to the mean of *gracilis* than it is to the mean of *hallowelli* (Table 5), and the mean of the ratio of tail length to total length of both sexes is within or very close to the diagnostic range for *gracilis* (Table 6).

Smith and Sanders (1952:218) pointed out an error in the range of subcaudals in female *T. g. gracilis* as stated in table 1 (p. 247) of Kirn *et al.* We

TABLE 6. Comparison of the Means of Some Characteristics of the Sample of *Tantilla gracilis* from Kansas (Our Data) with Some of the Diagnostic Characteristics (Kirn *et al.*, 1949:240) of *Tantilla gracilis gracilis*.

CHARACTERISTIC	Diagnostic range for *T. g. gracilis*	Mean of the sample ("*T. g. hallowelli*") from Kansas
No. of subcaudals..... males	40–50	48.4 (N=109)
Tail L./ Total L..... females	.160–.200	.20 (N=79)
Tail L./ Total L..... males	.200–.235	.23 (N=109)

add some additional corrections that should be made on the same page. In table two, column two ("Sex"), the words "male" and "female" are reversed for each characteristic. Also, in table two, column four ("Means from data of Force"), the means for caudals should be corrected from 33.61 to 43.61 in females and from 39.99 to 50.32 in males, as based on our recalculations from Force's data; we did not recalculate the means of Force's data for the other characteristics.

The discussion above demonstrates that the number of subcaudals and the ratio of tail length to total length are weak characteristics for diagnosing *T. g. gracilis* and *T. g. hallowelli.* The only remaining diagnostic characteristic given by Kirn *et al.* (1949) is the number of ventrals. Nevertheless, a step-cline in the number of ventrals, if one exists, is yet to be demonstrated. Therefore, we completely agree with Dowling (1957:32), who stated that ". . . the overlap in each character is so great that any subspecific differences appear to be as yet undefined. It is here suggested that *T. gracilis* be retained as binomial . . ."

LITERATURE CITED

Baird, S. F. and Girard, C.
1853. Catalogue of North American Reptiles in the museum of the Smithsonian Institution. Part I.—Serpents. Smithsonian Misc. Colls., 2:1-172.

Blanchard, F. N.
1938. Snakes of the genus *Tantilla* in the United States. Zool. Ser. Field Mus. Nat. Hist., 20(28):369-376.

Conant, R.
1958. A field guide to reptiles and amphibians. Houghton Mifflin Co., Boston, 366 pp.

Cope, E. D.
1900. The crocodilians, lizards, and snakes of North America. U. S. Nat. Mus. Rept. (1898), 153-1270.

Dowling, H. G.
1951. A proposed standard system of counting ventrals in snakes. British J. Herpetology, 1(5):97-99.
1957. A review of the amphibians and reptiles of Arkansas. Occas. Paps. Univ. Arkansas Mus., No. 3:1-51.

Dunn, E. R.
1928. A tentative key and arrangement of the American genera of Colubridae. Bull. Antivenin Inst. Amer., 2(147):18-24.

Force, E. R.
1935. A local study of the opisthoglyph snake *Tantilla gracilis* Baird and Girard. Papers Michigan Acad. Sci., Arts and Letters, 20:645-659.

Kirn, A. J., Burger, W. L., and Smith, H. M.
1949. The subspecies of *Tantilla gracilis*. Amer. Midl. Nat., 42(1):238-251.

Peters, J. A.
1960. The snakes of the subfamily Dipsadinae. Misc. Publs. Mus. Zool., Univ. Michigan, No. 114:1-224.
1964. Dictionary of herpetology. Hafner Publ. Co., New York, 392 pp.

Schmidt, K. P. and Davis, D. D.
1941. Field book of snakes. G. P. Putnam's Sons, New York, 365 pp.

Smith, H. M. and Sanders, O.
1952. Distributional data on Texan amphibians and reptiles. Texas J. Sci., 4(2):204-219.

Taylor, E. H.
1936. Notes and comments on certain American and Mexican snakes of the genus *Tantilla*, with descriptions of new species. Trans. Kansas Acad. Sci., 39:335-348.

Wright, A. H. and Wright, A. A.
1957. Handbook of snakes. Comstock Publ. Assoc., Cornell, Vol. II, pp. 565-1105.

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